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THE HYLID FROGS OF MIDDLE AMERICA

THE HYLID FROGS
OF
MIDDLE AMERICA

VOLUME 1

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PREFACE

Nearly two decades have passed since an undergraduate, who was primarily preoccupied with snakes at the time, attempted to identify some Mexican tree frogs and sought the aid of Professor Charles F. Walker. The latter offered assistance and encouragement, so that in time the student's field and laboratory studies turned more and more towards the anurans with special emphasis on the hylids. This fortuitous occurrence seemed trivial at the time, for the student in 1950, although his classroom daydreaming carried him far afield, could not begin to visualize the exciting experiences of the future. A year later the student found himself in México trodding paths through the mountains and discovering things new to him around every turn. The die was cast—an inescapable lure of the tropics, a lust that has intensified over the years.

Little did he realize that in the ensuing 15 years he would spend more than one thousand nights in the quest for the nocturnal songsters, whose calls he came to know as well as the physical features of the frogs themselves. Nor was it within his powers to foresee all of the wondrous aspects of nature in the tropics that would pass before his eyes.

There are few of the precious memories that can be transcribed adequately to paper, for it is difficult to describe in words such experiences as the grandeur of the forest at Laguna, the moonlight across Golfo Dulce, the awakening in a hammock to the gentle lapping of the waves on the beach of the Peninsula Valiente, the silence of the coniferous forest on Cerro Barolosa, the quetzals at Cerro Monte Cristo, the curious spider monkeys on Cerro Quia, the distant rumbling of erupting Volcan Irazú at night at La Palma, nor of the joy of having a peccary grace the meager food supplies, or of the aroma of a stewing tinamou, or of the smell of the rain in Chiriquí, the sunrise in the cold and dampness on Cerro de la Muerte, nor least of all the splendor of the sunset after the storm at Liberia.

The quest for tree frogs carried him to many strange places and provided him with many challenges, not the least of which was

travelling to the back country in search of specimens; travelling in much of Latin America cannot be appreciated by the uninitiated, who has not experienced the long hot trip on the flatcar from Arriaga to Tapachula, or the mudslide on the road to Puerto Escondido that temporarily stopped us and once we were through it took the truck that was following us over the mountain, or of careening down a mountain road in a second class Mexican bus whose brakes have just failed and the driver placing his passengers in the "hands of God." Nor is it possible for all persons to appreciate the long hours, nigh days, sitting in an uncomfortable saddle astride a mule plodding steadily across the mountains, as the wind blows your pancho and the rain runs down your neck, nor the three arduous days of pulling and pushing a *piragua* up the Río Tuira and how a month later we returned downstream through those same rapids in seven hours, nor of crossing Chiriquí Lagoon in a dugout in the fog and rain and how we ran aground twice on coral reefs, nor of flying to remote airstrips in overloaded Piper Cubs, whose pilots somehow always manage to miss the trees in the passes and find the small clearings casually referred to as airstrips. But even in this day of a variety of means of transportation the only way to many of the most interesting areas in Middle America is by foot, a time-honored method of travel, though at times painfully slow and arduous, nevertheless usually trustworthy. The days thus spent seem innumerable, perhaps only because of their apparent length, and are remembered for the steep ascent to Cerro Malí and how heavy our packs were when we reached the top, the scenic walk up the Río Tacarcuna until the river rose in flood and we made our last ford in water to our chests, the slippery roots that were used for foot-holds on Cerro Pando, and how after all day of slipping and sliding in the rain we reached our campsite on the Río Changena after dark and how two of our native packers came in later without their packs and we had to return for an hour's walk to fetch our sleeping gear.

He has been happy with his associations with many natives, who have provided a sepa-

rate, but enduring kind of education. How impressive were the *chicleros*' knowledge of the Petén forest and its inhabitants, or the Negros' ability at guiding the *piraguas* through the rapids in Darién, or the seemingly tirelessness of the packers on Cerro Mali. Memories of these people and others recall many incidents, many humorous, some happy, and a few sad, such as the sobering effect of the escape of a six-foot snake on the patrons of a small Mexican *cantina*, the singing of our *mozos* as we rode horseback across the Sierra de Coalcomán, the gleefulness with which Mayan children brought us specimens at Pisté, and the caution that our camp boys displayed when catching some animal that they thought to be venomous but moreso the board grins of satisfaction when they learned that they had found something valuable to us. The pleasant memories have been embellished with some misfortune, such as the revolution in Guatemala City with the smell of tear gas permeating the cool mountain air, the drunken Tarascans invading our camp and causing several frightful minutes of anxiety, the shooting and fires at the time of the Canal Zone crisis in 1964, but these are solely the everyday events of modern man.

Not all of the field work was easy; hardships are to be expected, and he would be remiss if he did not mention the mosquitos at Toocog that made our faces masses of lumps, or of the heat in the Tepalcatepec Valley, or of the cold on Volcán Barba and how the wind blew the rain level across the marsh there, or of losing our way in the swamp near Cosaleacaque and twisting and turning in mud and water for three hours before we came out, or of seeing a companion fall more than 30 feet from a tree, or having the logs break beneath his weight and lose his light and fall into a pool beneath a waterfall with darkness all around, or of having our clothing and sleeping bags partially eaten by ants. But all of these things are only indirectly related to tree frogs.

The search for tree frogs brought the student more than 10,000 specimens from Middle

America of all but a few of the known species of hylids, plus many other kinds of amphibians and reptiles. The rewards of the field work were gratifying, for the thrill of finding a rare or unknown species in its natural habitat is worth many hardships. But the search was not always successful, for how many times did he seek the rare *Plectrohyla avia* and then upon seeing his only individual, slip and fall in the stream and subsequently discover that the frog had moved away, not to be seen again, or of the four nights spent in the cloud forest on Cerro Uyuca and finding but two frogs, or of finally finding *Smilisca phaeota* calling in eastern Nicaragua, only to have the tape recorder cease to function, or of hearing unknown calls from the treetops and not being able to find the frogs, or of finding unknown tadpoles and having them die before reaching metamorphosis. These frustrations have been partially compensated by the collection of the second fringe-limbed *Hyla* in México, the discovery of the wierd spiny frog on Cerro Pando, the identification of the "treetop bopper" with the large *Gastrotheca ceratophrys*, and of ascending Cerro Monte Cristo for the purpose of obtaining recordings of *Hyla salvadorensis* and finding them calling in the last stream.

Perhaps the present generation of students in biology will not be so fortunate as to trod jungle pathways and see the living results of eons of natural selection, for in the minds of many scientists such mundane approaches to biological problems are history. But the student who was inspired to study tree frogs in 1950 is not displeased with himself for not having donned a white laboratory coat and synthesized proteins or attempted to crack the genetic code and scanned the output of a computer instead of the results of nature. In fact, he hopes to continue his pursuit of the tree frogs into South America where the fauna is even richer and more varied than in Middle America, but before he departs, he wishes to dedicate the present publication to an inspiring teacher, valued colleague, and good friend, Charles F. Walker.

William E. Duellman
Santa Cecilia del Río Aguarico,
Ecuador
June 21, 1968

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INTRODUCTION

When the first crossopterygian crawled out of the rich Devonian waters and cast the first envious vertebrate gaze at the terrestrial world, a boundless empire awaited colonization. Although the change from an ungainly lobe-finned locomotion to a terrestrial walking gait, enhanced and made possible by drastic modifications and even loss of precious bones, was agonizingly slow, generations succeeded generations, archetypes gave way to new evolutionary experiments, and the land became the home for the first quadrupeds—the amphibians. But this new environment was hostile to these aquatic emigrants who fought to avoid desiccation and faced the necessity to return to the water from which they had struggled in order to combine their genetic heritages in the production of a new generation. Some kinds, although they had developed lungs, eyelids, feet, and other assorted terrestrial adaptations, retreated to the placid life of the waters and slowly passed into evolutionary oblivion. Others faced the problems of terrestrial existence by developing armour and further invaded the land only to resign themselves to the inevitable return to the water to provide the continuation and eventual extinction of their own kind.

Somewhere, lost in the inextricable past of evolutionary history, one group of amphibians deviated from those who retired to their primordial home and from those who haphazardly rushed ahead without the advantage of the cleidoic egg. Perhaps at a time when the first reptilian rehearsal in thermoregulation was taking place or maybe at the time of the sprouting of the first mammalian hairs—it makes little difference—our little band of amphibian survivors struggled amidst a diverse lot of terrestrial creatures which had physiologically surpassed them.

Among the many unsolved evolutionary mysteries few tingle the imagination more than those interactions between the environment and the amphibian morphological adaptations—all unrecorded in the fossil record—that resulted in the reduction of the number of vertebrae, the fusion of the postsacral vertebrae into a long inflexible rod, the loss of the tail, and the development of extraordinary

long and powerful hind legs. Seemingly without predilection this group of amphibians leaped into the terrestrial scene, and the frog was born!

Such bizarreness of structure is equalled in the tetrapods only by the turtles; both groups have had an illustrious and successful existence. The relative triumph of the frogs in comparison with the amphibians of less radical posture is attested to by the vast array of living frogs, whereas most other groups of amphibians have long since abandoned their earlier conquests and remain now only as fragmentary designs in beds of shale. Not all non-saltatorial amphibians were so unfortunate, for by some unexplainable means a group of small, apparently relatively unmodified tailed forms survived to become salamanders and another group in a successful attempt to imitate earthworms lost their hard-earned limbs and took up a subterranean existence to survive as caecilians.

But frogs were not content just to be frogs. Although in the beginning they still were chained to the water for purposes of reproduction, they diversified and in so doing underwent many morphological and behavioral changes. They developed vocal cords and a membranous resonating chamber and learned to communicate, albeit crudely, but nevertheless effectively for their purpose. They continued their struggle against their aquatic bondage which they had inherited, and at several times in different places some of them broke the bonds and achieved terrestriality. But not all of the evolution was on land; the aquatic stages were not static. Swamps, lakes, marshes, and ponds were only the beginning. Rivers led away from the plains, and streams reached further into the highlands, where cold torrents awaited. By these aquatic avenues, dispersal was possible and life in new areas was achieved. And while the aquatic stages tested many schemes before developing the array of tadpoles known today, the frogs themselves hopped across the continents and reached every accessible corner of the globe where an ectotherm could live. Some settled in arid regions and modified their way of life and their structure so as to survive for months

on a small amount of invaluable water cleverly stored within their bodies. Others returned to the water and changed their ways to a strictly aquatic life, whereas most were content to remain on land and to utilize the marshes, swamps, streams, and forests for their abodes.

Some frogs explored the trees and found there an extensive and varied habitat, to which they adapted by modifying their fingers and toes, so as to be able to more effectively grasp the branches and leaves in their chosen home. One of these groups had an arciferal girdle and intercalary cartilages. Long after the evolution of these structures and the diversification of the group into perhaps 500 or so species, another highly successful evolutionary line listened to their nocturnal cacophony, instilled them in their stories and generations later studied them and called them Hyliidae.

Long before the amphibians arose, the earth was covered by extensive shallow seas separated by landmasses supporting only primitive plants. The imperceptible changes in the configurations of the land required millions of years during which time areas of land separated and drifted apart and the Atlantic Ocean was born between Africa and South America, and Australia and Antarctica shifted as Gondwanaland disappeared below the waters of the Indian Ocean. By one and one-quarter million years ago, in the Cretaceous, the continents of North America and South America were entirely separated from land in the rest of the world, except for an intermittent land bridge in the Bering Straits. At that time, North America was connected to South America by a narrow link—Central America.

Meager geological evidence indicates that in the upper Cretaceous, Central America was a moderately uplifted region enjoying equable climates. With the Laramide Revolution came changes—uplift of mountains, modification of climates, and consequent alteration of biotas. Sometime in the Eocene, the Bolivar Geosyncline resulted in the separation of South America from Central America and North America. Throughout the Tertiary, especially in the Miocene and Pliocene, dramatic disturbances greatly changed the Americas. Levels of the oceans rose and receded; the Rocky

Mountains and the Andes rose high above the clouds, and tropical climates retreated towards the lower latitudes leaving in some places nearly barren deserts in their wake. Recession of the seas and uplift of the land resulted in a reunification of South and Central America in the Pliocene. Mountains continued to rise, as volcanos rose and spewed ash and lava over much of Central America. These tortuous events were not halted during the Pleistocene when sea levels and water tables rose and fell, climates changed, and glaciers formed on the higher mountains.

The stage is basically the same, but the props have resulted in many different scenes. The hyliid frogs are among the actors in a drama that has been continuing for many, many millennia. We, the biologists, have been able to glimpse a moment of the play and are faced with the challenge of interpreting not only the present but all of the earlier scenes. I find the challenge exciting, but am envious of my readers, the critics.

The problems and principles of systematics and zoogeography are intricately amalgamated with those of evolution, the synthesis of all biology. The biochemists, physiologists, and embryologists can test many of their hypotheses by experimentation, but the conclusions of the systematists and zoogeographers can be reached only by observation, inferences, and extrapolation. New facts and interpretations continually result in minor additions to our knowledge and changes in our ideas. These facts and ideas emanate from the exploration of previously unstudied areas, the discovery of fossil faunas or even a single significant fossil, the intensive study of one or more biological problems in a single species or in an ecological community, and by the application of new methods of study.

New insights into old problems can be gained by applying new techniques to a large, diverse, and widespread natural group of organisms. Furthermore, the thorough study of the taxonomy and distribution of such groups provides the raw material for zoogeographic syntheses, which, in turn, can be applied to other groups of organisms. The conclusions of such studies each provides another small piece in the immense evolutionary puzzle.

The hyliid frogs are one of the most di-

verse and widespread families in the American tropics. Many of the species are common and easily studied; thus, the group affords an excellent subject for a systematic study. The size of the group—some 30 genera and perhaps 500 species—is too large to be treated monographically at one time. The results of my research presented here deal only with the species occurring in Middle America (México and Central America).

No comprehensive review of the Middle American hylids has been attempted previously, although revisions of some of the genera (Duellman, 1956a; Funkhouser, 1957; Duellman, 1963c; and Duellman and Trueb, 1966) have appeared. During the preparation of the present monograph, I have become painfully aware of the necessity of obtaining much additional knowledge on the much larger and more diverse South American hylid fauna, for therein lies the answer to many of the problems of relationships of the Middle American species.

Although I have a keen interest in hylid frogs that has become more intense in the past decade, I must confess that the study of the hylids was begun as a means to gain a better understanding of Middle American zoogeography. In a large measure the research has been successful in that regard. However, equally exciting has been the unraveling of a variety of problems concerning the taxonomy and life history of many of the species.

The purposes of the present publication are to 1) Describe accurately the taxa of Middle American hylid frogs and provide a means for their identification, 2) Assay the phylogenetic relationships of the genera and species, and 3) Evaluate the phylogenetic relationships and distributional data in a zoogeographic synthesis. The taxonomic methodology utilized has included the usual array of external morphological characters, including wherever possible coloration in life, plus cranial osteology, tadpole morphology, mating calls, chromosome number, and various aspects of the ecology, behavior, and life history.

My ideas on phylogenetic relationships differ markedly from some of those presented by other workers. This is due principally to the fact that most earlier workers did not

utilize characteristics of the tadpoles, cranial osteology, and mating calls, all of which I have found to be extremely useful in determining relationships. In synthesizing the distributional and phylogenetic data I have critically reevaluated the generally accepted zoogeographic "truths" on the basis of new information, both biological and geological. Thus, by taking the attitude that nothing is sacred, I have come up with some interpretations that strongly differ from previous ideas. Perhaps my colleagues and succeeding generations of biologists will find some of my thoughts more than amusing and maybe even useful and justifiable.

Probably every author of a systematic monograph wishes that his published results could be the "last word" on the group, but such is never the case. I am certain that additional species await discovery in Middle America and that the information provided by such unknown species will alter some of my groupings and ideas of relationships. The discovery of tadpoles and analysis of calls still unknown to me most likely will result in further revisions. Thus, I beg my readers not to judge my work too harshly and to remember that the material presented here makes their critical evaluation of new, as well as old, material a much easier task.

ACKNOWLEDGMENTS

The report of my researches embodied in the following pages is the result of innumerable kindnesses and cooperation of many colleagues, associates, assistants, friends, and even total strangers. Through the years of my active work on the hylid frogs my debt of gratitude has grown to enormous proportions and were I to acknowledge each person adequately for his or her favors, I am afraid that I would have little or no room left for the frogs.

During the past decade I have borrowed and even reborrowed hundreds of specimens from many collections and have visited all major collections in the United States at least once. For their efforts in my behalf, either by providing working space in their laboratories, loaning specimens to me, or both, I am grateful to Sr. Ticul Alvarez, Sr. Miguel Alvarez del Toro, Dr. Richard J. Baldauf, Dr. W.

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Although most of the colored photographs of frogs on which the colored plates were based were taken by me, some additional photographs—some of species that I did not have—were generously provided by Dr. Kraig Adler, Dr. Charles M. Bogert, Dr. Richard B. Loomis, Dr. John D. Lynch, Dr. Charles W. Myers, and Dr. Richard G. Zweifel. Dr. Loomis and Dr. David L. Jameson also provided living frogs for illustrative purposes, and Dr. Myers contributed photographs reproduced herein as black and white plates.

My work on the analysis of the mating calls was enhanced through the loans of tapes from Dr. W. Frank Blair, Dr. Charles M. Bogert, Dr. W. Ronald Heyer, Dr. David L. Jameson, Dr. Kenneth R. Porter, and Dr. Richard G. Zweifel.

Several persons contributed information from their own observations and gave me access to their field notes; thusly, I am indebted to Dr. Kraig Adler, Dr. Jay M. Savage, Dr. Laurence C. Stuart, Dr. Charles F. Walker, Dr. Richard G. Zweifel, and especially Dr. Charles W. Myers. Furthermore, Dr. Savage made available to me manuscripts on aspects of his work on Costa Rican frogs and Dr. Alan E. Leviton provided helpful data on *Hemiphractus*. Dr. William F. Pyburn provided tadpoles of two species.

Had the collection of all of the data and specimens been left to me alone, the amount of available material would be considerably less than now exists. Several of my associates and students at the University of Kansas suf-

fered long hours of hardship, often under most unpleasant conditions, in assisting me in the field or working independently in the field. For their efforts, I am grateful to Dr. Charles J. Cole, Dr. Arthur C. Echternacht, Dr. Laurence M. Hardy, Mr. Richard L. Holland, Mr. Dale L. Hoyt, Sr. Juan R. León, Dr. John D. Lynch, Dr. Craig E. Nelson, Dr. Jerome B. Tulecke, and Dr. John Wellman. Dr. Charles W. Myers and Dr. Linda Trueb were the greatest contributors in the field; together, often guided solely by Pan, we trod many distant ridges and explored many swamps and cascading streams; their aid and companionship cannot be adequately acknowledged by words alone. I am also grateful to Dr. J. Knox Jones, Jr. and Dr. James D. Smith, who in the course of their field work on mammals in Central America, took the time to collect many valuable frogs. My own field work was furthered by helpful suggestions by persons familiar with certain areas. Dr. Charles M. Bogert, Dr. Norman Scott, and Dr. Laurence C. Stuart directed me to choice localities in Oaxaca, Costa Rica, and Guatemala, respectively.

Field work in the Middle American countries was made possible by the generous cooperation of government officials, especially Ing. Rodolfo Hernandez Corzo of the Dirección General de Caza in México and Sr. Jorge Ibarra, Director of the Museo Nacional de Historia Natural in Guatemala. Ing. Julio Aguirre C. provided comfortable working quarters at the Instituto Tropical de Investigaciones Científicas in San Salvador and provided guides and transportation to the mountains of northern El Salvador. Dr. Robert Armour, Assistant Director of the Escuela Agrícola Panamericana at El Zamorano, Honduras, graciously provided plush quarters at the school and arranged for our stay on Cerro Uyuca. Dr. Alvaro Wille of the Universidad de Costa Rica provided invaluable aid in that country in 1961; at the same time Dr. Robert Hunter arranged for quarters at the Instituto Interamericano de Ciencia Agrícolas at Turrialba and provided housing at Puerto Viejo. In 1965 and 1966, field work was facilitated by Dr. Stephen B. Preston of the Organization of Tropical Studies. Work in Panamá was greatly facilitated by the cooperation of Mr.

Marvin Keenan of the United States Army Environmental Health Unit at Fort Clayton, Dr. Martin H. Moynihan and Dr. Neal G. Smith of the Smithsonian Institute for Tropical Research, and Dr. G. B. Fairchild and Dr. Martin D. Young of the Gorgas Memorial Laboratory. In addition, the field work was successful due to the kindnesses of many local residents, who provided housing, transportation, guides, and often valuable specimens. Their generosity will be remembered long after the details of the frogs are forgotten.

In the laboratory Miss Martha Crump and Mr. Bruce Curfman aided in collecting and tabulating data. Miss Crump and Mr. Robert R. Patterson prepared the osteological specimens, and Dr. Gerald R. Smith took necessary radiographs. To them I am deeply grateful for shortening my months of drudgery.

The osteological data presented herein is the work of Dr. Linda Trueb, who examined all of the osteological material, aided in defining the groups, and helped me formulate the concepts of phylogenetic relationships. Her contributions to the study represent many laborious hours and a great deal of thought.

I owe thanks to Mr. Jeffry Allen and Mr. Tom Swearingen for preparing the final maps and graphs. All line drawings and tone and color drawings reproduced as plates are the careful work of Mr. David M. Dennis. I have been fortunate to have such a skillful illustrator. Furthermore, I am grateful to Mr. Elmo Reiff of the Mid-Continent Engraving Company, who provided much technical advice and painstaking care on the reproduction of the colored illustrations.

A scientific paper of this magnitude can result only from the efforts of a skilled secretary. I have been fortunate in having the determined assistance of Mrs. Donna L. Ford, who transcribed my recorded text, corrected my grammar, proofread the copy, and then faithfully reproduced the final draft. She has my most profound thanks.

Dr. Linda Trueb critically read the entire manuscript. Various sections of the manuscript were read by Sr. Juan R. León, Dr. John D. Lynch, Dr. Charles W. Myers, Dr. Laurence C. Stuart, Dr. Charles F. Walker, and Dr. Richard G. Zweifel. I am grateful for their comments and emphasize that errors of

commission and omission are my responsibility alone.

Throughout the course of my work on the hylid frogs at the University of Kansas, I have been fortunate in being associated with considerate administrators. Dr. E. Raymond Hall, former Director of the Museum of Natural History, and Dr. A. Byron Leonard, former Chairman of the Department of Zoology, have released me from duties and helped to arrange my schedule so that I could spend long periods of time in the field. Their enlightened attitudes made much of the work possible. I am indebted to Dr. Philip S. Humphrey, Director of the Museum of Natural History, and to Mr. Irvin E. Youngberg of the Endowment Association, University of Kansas, for their encouragement and assistance in bringing this work to completion.

For eight years, my research on Middle American hylid frogs was supported by grants (G-9827, GB-1441, and GB 5818) from the Biomedical Sciences Section of the National Science Foundation. The publication of the colored plates was made possible by a grant (GN-640) from the Office of Science Information Service of the National Science Foundation. In this era of world crises it is comforting to realize that the people of our nation through government agencies support a vast array of pure research. I only hope that in due time the results in the present publication will justify part of the monetary expenditure.

MATERIALS AND METHODS

The material basis for this report is a total of 32,569 museum specimens of the 115 species of hylid frogs from Middle America, the accompanying field notes on many of these specimens, and recordings of their mating calls. I have examined 31,327 preserved frogs, 575 skeletons, 591 lots of tadpoles and 76 clutches of eggs of hylids from Middle America, plus several hundred specimens from South America and some from the United States. The field work by my associates and me in Middle America resulted in the collection of approximately 12,000 of these specimens, most of which are preserved in the Museum of Natural History at the University of Kansas.

All frogs collected by me and my associates were preserved in 10 per cent formalin and later transferred to 70 per cent ethyl alcohol. Specimens were fixed in trays with the knees spread, heels together, and fingers and toes spread, plantar surfaces down. Dried skeletons were prepared from preserved specimens or by means of dermestid beetles from carcasses dried in the field. Skeletal preparations of small specimens (less than 40 mm. snout-vent length) were made by clearing the frogs in potassium hydroxide, staining the bones with alizarin red, destaining in potassium hydroxide, and storing them in glycerin. Dried skeletons were found to be wholly unsatisfactory for small species; when sufficient material was available, both dried and cleared and stained skeletal preparations were made of species having snout-vent lengths of 40 to 60 mm. All eggs and tadpoles were fixed and stored in 10 per cent formalin. Proper preservation of tadpoles is possible only if the specimens are not crowded in the container; preferably the original preservative is replaced with fresh formalin after about 24 hours.

Measurements were taken with dial calipers and recorded to the nearest 0.1 mm. When possible, I measured only specimens that were fixed in the manner just described (usually those collected by me and my field associates). I found that measurements taken on uniformly preserved specimens were subject to less variation than those on specimens fixed in various ways. Measurements usually were taken on one series of 20 to 25 males and as many females as available from a single locality. When sufficient specimens were not available from one locality, a sample was assembled from several localities in one area. In wide ranging species and in species having disjunct ranges, measurements were taken on samples from various parts of the range. Throughout the text several ratios of measurements to snout-vent length are given; where these ratios are tabulated, snout-vent length is abbreviated S-V L.

Developmental stages of tadpoles were determined from Gosner's (1960) developmental tables.

In the course of my work on Middle American hylids, I have analyzed 731 record-

ings of 76 species. Most of these recordings are in the bioacoustics laboratory in the Museum of Natural History at the University of Kansas, but I have also utilized tapes from the collection at the University of Texas and at the American Museum of Natural History, plus a few tapes in the collection in the Museum of Zoology at the University of Michigan. My recordings were obtained by using a Magnemite (Model 610E and 610EV) with a tape speed of 15 inches per second, and a Uher (Model 4000-S) with a tape speed of 7½ inches per second. Audiospectrograms were made on a Vibralyzer (Kay Electric Company). The audiospectrograms reproduced here as plates 12-40 were all made using the narrow band of frequency. I have found that these displays more accurately show the nature of the call than do the wide band displays; this is especially true of the sections of the calls. In some cases, it is difficult or impossible to determine the pulse rate from audiospectrograms made on the narrow band frequency; in those cases, I made wide band audiospectrograms for purposes of determining pulse rate, but these have not been reproduced in the plates. Characteristics and measurements of the calls were obtained by using a grid marked on a plastic overlay on top of the audiospectrograms. In tables, cycles per second is abbreviated cps.

The synonymy given at the beginning of each generic account includes only references to the original description of the genus and other genera that are considered to be synonymous. The type species is listed for each.

The synonymies at the beginning of each species account include the reference to the original description of that species and all other species and subspecies that are considered to be junior synonyms. In addition, the following standard references on Middle American hylids are listed, where appropriate, in the synonymies: Boulenger (1882a), Brocchi (1882), Günther (1885-1902), Kellogg (1932), Smith and Taylor (1948), Stuart (1963), and Taylor (1952c). References to each generic and specific, or subspecific, combination of names is given. Furthermore, if the species is included in a group that has been recently revised or monographed, a reference to such

publication is given. The synonymies are annotated to include the catalogue number and depository of type specimens, the type locality, and the collector of the type specimens. The synonymies also contain references to publications in which names are synonymized or transferred from one genus to another.

All references in a synonymy are given only to author, date, and page. The complete citations for these references are given in the Literature Cited.

The locality records for the various species and subspecies have been plotted on maps. All localities that could be found have been plotted, but due to the crowding of symbols, some localities have been covered by one symbol. The Map of Hispanic America (Scale 1:1,000,000) published by the American Geographical Society has been my primary source, but other maps and atlases have been consulted.

Specimens examined are listed in Appendix I. Throughout the text and appendices, specimens are listed with their catalogue numbers and abbreviations for the museum or private collections, as follows:

- A.M.N.H., The American Museum of Natural History
 A.N.S.P., Academy of Natural Sciences of Philadelphia
 B.M.N.H., British Museum (Natural History), London
 B.Y.U., Brigham Young University
 C.A.S., California Academy of Sciences
 C.J.G., Coleman J. Goin, Gainesville, Florida
 C.M., Carnegie Museum, Pittsburgh
 E.H.T.-H.M.S., Edward H. Taylor-Hobart M. Smith, Lawrence, Kansas
 F.A.S., Frederick A. Shannon, Wickenburg, Arizona
 F.M.N.H., Field Museum of Natural History
 G.M.L., Gorgas Memorial Laboratory, Panama City
 I.P.N., Instituto Politecnico Nacional, Mexico City
 K.U., University of Kansas Museum of Natural History
 L.A.C.M., Los Angeles County Museum
 L.B.S.C., Long Beach State College
 L.S.U., Louisiana State University, Museum of Zoology
 M.C.Z., Museum of Comparative Zoology, Harvard
 M.d.L.S., Museo de La Salle, Bogotá, Colombia
 M.M., Magdeburg Museum, Germany
 M.N.H.N., Museum National d'Histoire Naturelle, Paris
 M.V.Z., Museum of Vertebrate Zoology, Berkeley
 M.Z.T.G., Museo de Zoología Tuxtla Gutierrez, México
 N.H.R.M., Naturhistoriska Riksmuseet, Stockholm
 N.M.W., Naturhistorisches Museum Wien, Vienna
 R.C.T., Richard C. Taylor, Lawrence, Kansas
 R.H., Ratibor Hartmann, Finca Santa Clara, Panamá
 S.D.N.H.M., San Diego Natural History Museum
 S.N.M., Senckenbergische Natur-Museum, Frankfurt-am-Main, Germany
 S.U., Stanford University
 T.C.W.C., Texas Cooperative Wildlife Collection, Texas A&M University
 T.N.H.M., Texas Natural History Museum, University of Texas
 U.C.R., Universidad de Costa Rica, San José
 U.F., University of Florida
 U.I.M.N.H., University of Illinois Museum of Natural History
 U.M.M.Z., University of Michigan Museum of Zoology
 U.N.M., University of New Mexico
 U.S.C., University of Southern California
 U.S.N.M., United States National Museum
 U.U., University of Utah
 Z.M.B., Zoologisches Museum, Berlin

The color illustrations (pls. 41-72) are water-color reproductions drawn from color transparencies taken in the field, principally by the author, with a Kine Exacta camera. The four-color engravings were made at the Mid-Continent Engraving Company in Wichita, Kansas. The individual figures on each color plate are identified only to species and scale. The museum number and locality for the specimens depicted in the plates are given in Appendix 2.

HISTORICAL RESUMÉ

A review of the history of our knowledge of Middle American hylids reveals that there have been three major periods. During the first period (1853-1900) most of the work on hylids was done by a few herpetologists—chiefly George A. Boulenger, Paul Brocchi, Edward D. Cope, and Albert C. L. Günther—working with relatively few specimens collected by other persons. These workers seldom had any knowledge of the appearances of the frogs in life, nor did they possess much, if any, information on the habitats or life histories of the frogs. During the second period (1920-1941) an increased number of herpetologists worked on Central American hylids, and the chief contributors to our knowledge—Emmett R. Dunn, Karl P. Schmidt, Hobart M. Smith, Laurence C. Stuart, and Edward H. Taylor—collected most of their own material; consequently, new kinds of data (colors in life, habitats, and life histories) were utilized. The third period (1947-present) is an intensified continuation of the second period. However, the third period differs from the others by being a time of synthesis and interpretation, which has been made possible by quantities of specimens, knowledge of the frogs in their natural environments, and the utilization of new kinds of information, such as voice analysis, cytogenetics, and comparative osteology.

Herpetological exploration in Middle America lagged behind that in North and South America by about half a century. Linnaeus (1758) and Laurenti (1768) named several species of South American frogs; many of these were based on illustrations in Seba's (1734) "Thesaurus." Three species—*Hyla boans*, *H. rubra*, and *Phrynohyas venulosa*—occur in Central America. Spix (1824) and Wied (1824b) named several species of frogs from South America; of those named, *Hyla crepitans* Wied, occurs in Central America.

Many herpetological specimens were obtained for the United States National Museum by various members of the field parties conducting the United States and Mexican Boundary Survey from 1851 to 1854. These collections provided the type specimens of *Hyla affinis* and *H. vanvlietii* Baird (1854) and *Hyla nebulosa* Hallowell (1854).

The first species of hylid named from Middle America was *Hyla baudinii* from "Mexique" (Duméril and Bibron, 1841); the type is in the Museum National d'Histoire Naturelle in Paris. Another collection received by the museum in Paris was made by Arthur Morelet in El Petén and Alta Verapaz, Guatemala; his collection contained the specimens that became the type of *Hyla moreletii* (Duméril, 1853). Major William Rich sent a collection of amphibians from Mexico City to the United States National Museum in 1853. In the collection were two specimens that became the syntypes of *Hyla eximia* Baird (1854). Baron J. von Warzewicz made important botanical collections and obtained many species of amphibians in western Panamá. The amphibians were sent to the Krakow Museum in Poland. Oscar Schmidt (1857) gave brief Latin diagnoses for several new species, including *Hyla molitor*, *H. pugnax*, and *H. splendens*, and in 1858 provided extensive descriptions and illustrations of the new species. Some of Warzewicz's collection reached the Zoologisches Museum in Berlin; Wilhelm Peters (1863) named *Hyla sordida* from "Veraguas," Panamá. Other collections were received in Berlin, and among the new species named from México was *Hyla microtis* Peters.

The most prolific writer on Middle American hylids in the last half of the Nineteenth Century was Edward D. Cope, who between 1862 and 1894 named 31 species and five genera of hylid frogs from Middle America. Among Cope's more important contributions are his report on the Costa Rican collections made by William M. Gabb and the Nicaraguan collections assembled by J. A. McNeil and J. F. Bransford. Most of the collections studied by Cope had been received by the United States National Museum; most of the types of Cope's species are in that museum, but some are in the Academy of Natural Sciences of Philadelphia, whereas the location of others is unknown.

The first Middle American hylids to reach the British Museum apparently were those in a collection made by Auguste Sallé in Veracruz, México; specimens in this collection formed the type series of *Hyla euphorbiacea* Günther, 1859. At about this time Osbert

Salvin and Frederick D. Godman initiated their expeditions to México and northern Central America. Salvin's first trip to Alta Verapaz, Guatemala, resulted in the description of *Hyla holochroa* (Salvin, 1860). Godman and various associates (Herbert H. Smith, C. T. Hoege, and Mateo Trujillo) collected in many parts of southern México; Salvin and Godman both collected in Guatemala and other parts of Central America; in later years (1879 and 1880), O. C. Champion continued their field work in Guatemala (see Godman, 1915, for itineraries). Alphonso Forrer made important collections from Sinaloa, México. The explorations by Salvin and Godman, and their associates, resulted in the material basis for the "Biologia Centrali-Americana." Albert C. L. Günther prepared the volume on the reptiles and amphibians, which was issued in parts between 1885 and 1902 (accounts of 48 hylids in 1901 and 1902). By this time the explorations in Middle America had acquired specimens that became the types of 14 species named by Günther and George A. Boulenger; the latter included much of the new material in his "Catalogue of the Batrachia Salientia . . ." published in 1882, in which he listed 38 species of hylids from México and Central America.

The counterpart of the British biological investigation in Middle America was the French "Mission Scientifique au Mexique et dans l'Amérique Centrale" decreed by Napoleon III in 1864. Marie-Firmin Bocourt was the chief naturalist attached to the commission, and Adolphe Boucard was a member of at least one of the exploration parties, which worked in México and Guatemala from 1865 to 1867. All of the specimens were deposited in the Museum National d'Histoire Naturelle in Paris. The amphibians were studied by Paul Brocchi, who published descriptions of five new species in 1877 and 1879 and summarized the amphibians of the *Mission Scientifique* in his "Étude des Batraciens de l'Amérique Centrale," published in 1882. Brocchi listed 31 species of hylids. Additional Mexican specimens were reported by M. F. Mocquard in 1889.

Thus, at the dawn of the Twentieth Century the first period of herpetological exploration had been completed. The new century

witnessed only the minor amphibian collections made by Edward W. Nelson and Edward A. Goldman in México (reported by Remington Kellogg in 1932) and a few small collections sent to the United States National Museum where Leonhard Stejneger (1906, 1911, and 1917) named four species of hylids. Essentially for the first quarter of the Twentieth Century, the fertile herpetological fields of Middle America lay fallow, except that the American Museum of Natural History sent an expedition to the Caribbean lowlands of Nicaragua in 1916; the amphibians were reported on by Noble (1918). Many amphibians were obtained in Darién, Panamá, by Charles M. Breder, Jr. as a member of the Marsh-Darién Expeditions of The American Museum of Natural History in 1924; Emmett R. Dunn (1934) named one new species of *Hyla* from the collection, and Breder (1946) presented a summary of the life history data.

Between the late 1920's and World War II, North American herpetologists began a second biological conquest of Middle America. Emmett R. Dunn explored the fauna in Costa Rica and Panamá, and Karl P. Schmidt made important collections in Guatemala and Honduras. Between them, they discovered and named seven new hylids from Central America in as many years. The collections made by Dunn were deposited in the Academy of Natural Sciences of Philadelphia, the American Museum of Natural History, and the Museum of Comparative Zoology at Harvard University, whereas those made by Schmidt were deposited in the Field Museum of Natural History.

The first Mexican expedition by the Museum of Zoology at the University of Michigan was conducted by Alexander G. Ruthven in 1911, and Helen T. Gaige collected in Panamá in 1923, but that institution did not intensify its Middle American program until the 1930's. James A. Oliver made important collections in Colima, México, in 1935 and with Norman Hartweg studied the herpetofauna of the Pacific slopes of the Isthmus of Tehuantepec, México. In 1940 and 1941, Hartweg made important collections in Chiapas. In 1933, Laurence C. Stuart began his studies of the Guatemalan herpetofauna that have continued to the present time and resulted in many

faunal studies, descriptions of new species (including four *Plectrohyla* and one *Ptychohyla*), and in 1963, a checklist of the Guatemalan herpetofauna.

In 1932, Edward H. Taylor initiated his studies on the amphibians and reptiles of México. Joined in his researches by Hobart M. Smith, he named and described 24 species of Mexican hylids from 1937 to 1945. From 1939 to 1941, Smith collected in México under the auspices of the Walter Rathbone Bacon Travelling Fellowship of the Smithsonian Institution. The large collections of amphibians were deposited, for the most part, in the United States National Museum and reported on by Taylor and Smith (1945). The earlier material collected in México by Smith and Taylor formed a part of the Edward H. Taylor-Hobart M. Smith collection. Approximately half of this collection was later deposited in the Museum of Natural History at the University of Illinois; in 1959, most of the other half was sold to the Field Museum of Natural History. The amphibian fauna of México was summarized by Smith and Taylor in 1948; they listed 55 species of hylids from México.

After World War II, with the advent of new roads in Middle America and financial support for biological investigations, herpetologists began swarming into México in the late 1940's and into Central America about a decade later. Laurence C. Stuart continued his studies in Guatemala, whereas Edward H. Taylor began a study of the herpetofauna of Costa Rica. Taylor collected in Costa Rica in 1947, 1951, 1952, and 1954; his collections were deposited in the Museum of Natural History at the University of Kansas. In 1947, Taylor was accompanied by Richard C. Taylor, who kept his collections apart from those deposited at the University of Kansas. Later R. C. Taylor's collections were sold to the Field Museum of Natural History. Taylor (1952c, 1954b, 1955, and 1958) reviewed the amphibians of Costa Rica and named 15 species of hylids.

The post-war period of discovery has continued to the present time due to efforts of collectors in reaching isolated areas that previously had not been collected. Most of the species of hylids named from Middle

America in the past decade are montane species. By 1968, 187 hylid frogs had been named from Middle America (fig. 1; table 1).¹ The trend curve for the rate of species description of Middle American hylids is nearly like that for the entire family throughout its world-wide range (Steyskal, 1965).

In the 1950's began a period of synthesis and review of genera and species groups; thus, the genus *Phrynohyas* was reviewed by Duellman (1956a), *Phyllomedusa* by Funkhouser (1957), *Ptychohyla* by Duellman (1963c), and *Smilisca* by Duellman and Trueb (1966). The University of Michigan and the University of Illinois continued to concentrate on the Mexican and Guatemalan faunas, and a group of biologists at the University of Southern California, under the enthusiastic direction of Jay M. Savage, began an intensive study of the Costa Rican herpetofauna. The early post-war emphasis at the University of Kansas was on México and Costa Rica; but later the work in México diminished as Central American areas were emphasized.

Excellent collections of Middle American hylids are present in North American museums, but pitifully few specimens are represented in Middle American collections. The Instituto Politecnico Nacional and the Museo de Zoología de Tuxtla Gutierrez in México, the Museo Nacional de Historia Natural in Guatemala, the Instituto de Investigaciones Tropicales at the Universidad de El Salvador, the Museo de Zoología de la Universidad de Costa Rica, and the Gorgas Memorial Laboratory in Panamá have small collections.

In the past decade we have observed a change from museum-oriented work to field-oriented research. Increasingly more atten-

¹ Two specific names originally proposed in the genus *Hyla* in Middle America are now considered to belong to the leptodactylid genus *Eleutherodactylus*. These are *Hyla punctariola* O. Schmidt (1857) and *H. chica* Noble (1918); the latter is a synonym of *Eleutherodactylus diastema*. Günther (1901) named *Hyla mocquardi* from "Guatemala or Panama"; Duellman (1968c) showed that *mocquardi* was a member of the South American *Hyla pulchella* group and should not be considered as a member of the Middle American herpetofauna. Taylor (1952a) named *Hyla shrevei* from Panamá; Goin (1959) demonstrated that the type of *shrevei* was actually a mislabeled *Hyla wilderae*.

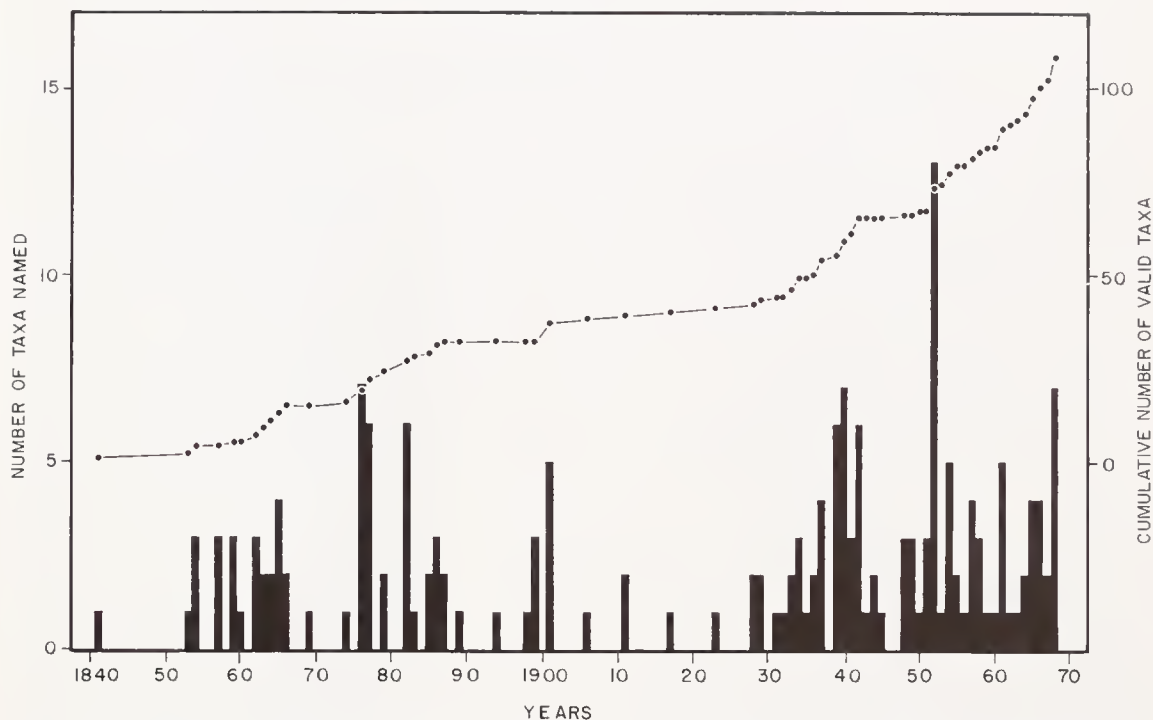


FIG. 1. Number of species and subspecies of hylid frogs named from Middle America from 1841 through 1968. The bars represent the number of names proposed in each year; the line represents the cumulative number of taxa considered to be valid. Middle American taxa discovered in, and named from, the United States and from South America, replacement names for earlier names that are preoccupied, and *nomina nuda* are not included; *nomina dubia* are not included in the line.

tion is being given to life histories (Starrett, 1960a) and interactions between species, especially regarding the importance of voice in frogs (Fouquette, 1960b; Duellman, 1967c). These kinds of studies have complemented the faunistic surveys and have added a wealth of supplemental data to museum specimens.

My own early work in Middle America was not directed towards the study of hylid frogs, although an interest in these frogs soon developed. My first collections in México were made in the summer of 1951, when I traversed the Sierra de Coalcomán in Michoacán to the Pacific coast and also worked briefly in Nayarit. In 1955, I returned to western México for two months and collected in the Tepalcatepec Valley and the Sierra de Coalcomán in Michoacán and briefly at Oaxaca and Tehuantepec in the state of Oaxaca. Seven months were spent in México in 1956; the country was traversed in both rainy and dry seasons, and only the peninsulas of Baja California and Yucatán were neglected. January and early

February of 1958 were spent in the cloud forests of eastern México in an effort to secure hylids. The same areas were worked again during a two-month visit to México in the summer of 1958, but most of the time was spent in the Isthmus of Tehuantepec. In March and April of 1959 a brief, but profitable, trip was made into the Sierra de Juárez in northern Oaxaca. All material collected up to that time was deposited in the Museum of Zoology at the University of Michigan.

In September, 1959, my studies on the Middle American hylid frogs received support from the National Science Foundation and were centered at the Museum of Natural History at the University of Kansas. All specimens henceforth collected were deposited in that museum. A brief trip was made to the cloud forests of eastern México in December, 1959; I was accompanied by Dale L. Hoyt and John Wellman, and we succeeded in obtaining needed material of the *bistincta*, *miotympanum*, and *taeniopus* groups of *Hyla*. In February and March, 1960, J. Knox Jones, Jr. and

TABLE 1
 Alphabetical Synonymy of Middle American Hyliid Frogs

Trivial name, original generic name, author, and date	Present name
<i>adipoventris</i> (<i>Ptychohyla</i>) Taylor, 1944	<i>Ptychohyla leonhardschultzei</i>
<i>affinis</i> (<i>Hyla</i>) Baird, 1854 (<i>nec</i> Spix)	<i>Hyla arenicolor</i>
<i>alcorni</i> (<i>Agalychnis</i>) Taylor, 1952	<i>Pachymedusa dacnicolor</i>
<i>alleei</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla uranochroa</i>
<i>altae</i> (<i>Hyla</i>) Dunn, 1933	<i>Hyla staufferi altae</i>
<i>altipotens</i> (<i>Hyla</i>) Duellman, 1968	<i>Hyla altipotens</i>
<i>alvaradoi</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla colymba</i>
<i>angustilineata</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla angustilineata</i>
<i>annae</i> (<i>Phyllomedusa</i>) Duellman, 1963	<i>Agalychnis annae</i>
<i>arborescendens</i> (<i>Hyla</i>) Taylor, 1939	<i>Hyla arborescendens</i>
<i>arboricola</i> (<i>Hyla</i>) Taylor, 1941	<i>Hyla eximia</i>
<i>arenicolor</i> (<i>Hyla</i>) Cope, 1866	<i>Hyla arenicolor</i>
<i>avia</i> (<i>Plectrohyla</i>) Stuart, 1952	<i>Plectrohyla avia</i>
<i>axillamembrana</i> (<i>Hyla</i>) Shannon and Werler, 1955	<i>Hyla loquax</i>
<i>azteca</i> (<i>Hylella</i>) Taylor, 1943	<i>Hyla smaragdina</i>
<i>baudinii</i> (<i>Hyla</i>) Duméril and Bibron, 1841	<i>Smilisca baudinii</i>
<i>beltrani</i> (<i>Hyla</i>) Taylor, 1942	<i>Smilisca baudinii</i>
<i>biseriata</i> (<i>Hyla euphorbiacea</i>) Lynch, 1964	<i>nomen nudum</i>
<i>bistincta</i> (<i>Hyla</i>) Cope, 1877	<i>Hyla bistincta</i>
<i>bivocata</i> (<i>Hyla</i>) Duellman and Hoyt, 1961	<i>Hyla melanomma bivocata</i>
<i>boans</i> (<i>Rana</i>) Linnaeus, 1768	<i>Hyla boans</i>
<i>bocourti</i> (<i>Hyla</i>) Mocquard, 1899	<i>Hyla euphorbiacea</i>
<i>bogertae</i> (<i>Hyla</i>) Straughan and Wright, 1969	<i>Hyla bogertae</i>
<i>bogerti</i> (<i>Ptychohyla</i>) Taylor, 1949	<i>Ptychohyla euthysanota euthysanota</i>
<i>boulengeri</i> (<i>Scytotis</i>) Cope, 1887	<i>Hyla boulengeri</i>
<i>brachycephala</i> (<i>Plectrohyla</i>) Taylor, 1949	<i>Plectrohyla matudai</i>
<i>bromeliacia</i> (<i>Hyla</i>) Schmidt, 1933	<i>Hyla bromeliacia</i>
<i>bromeliana</i> (<i>Hyla</i>) Taylor, 1939	<i>Hyla taeniopus</i>
<i>bufonia</i> (<i>Hyla</i>) Spix, 1824	<i>Phrynohyas venulosa</i>
<i>cadaverina</i> (<i>Hyla</i>) Cope, 1866	<i>Hyla cadaverina</i>
<i>calcarifer</i> (<i>Agalychnis</i>) Boulenger, 1902	<i>Agalychnis calcarifer</i>
<i>californiae</i> (<i>Hyla</i>) Gorman, 1960	<i>Hyla cadaverina</i>
<i>callidryas</i> (<i>Hyla</i>) Cope, 1862	<i>Agalychnis callidryas</i>
<i>cardenasi</i> (<i>Hyla</i>) Taylor, 1939	<i>Hyla eximia</i>
<i>ceratophrys</i> (<i>Hyla</i>) Stejneger, 1911	<i>Gastrotheca ceratophrys</i>
<i>chamulae</i> (<i>Ptychohyla</i>) Duellman, 1961	<i>Ptychohyla schmidtorum chamulae</i>
<i>chaneque</i> (<i>Hyla</i>) Duellman, 1961	<i>Hyla chaneque</i>
<i>charadricola</i> (<i>Hyla</i>) Duellman, 1964	<i>Hyla charadricola</i>
<i>cherrei</i> (<i>Hyla</i>) Cope, 1894	<i>nomen dubium</i>
<i>chryses</i> (<i>Hyla</i>) Adler, 1965	<i>Hyla chryses</i>
<i>clarkii</i> (<i>Helocaetes</i>) Baird, 1854	<i>Pseudacris clarkii</i>
<i>colymba</i> (<i>Hyla</i>) Dunn, 1931	<i>Hyla colymba</i>
<i>copii</i> (<i>Hyla</i>) Boulenger, 1887	<i>Hyla arenicolor</i>
<i>corasterias</i> (<i>Phrynohyas</i>) Shannon and Humphrey, 1957	<i>Phrynohyas venulosa</i>
<i>coronata</i> (<i>Gastrotheca</i>) Stejneger, 1911	<i>Anotheca spinosa</i>

TABLE 1—(Continued)

Trivial name, original generic name, author, and date	Present name
<i>cotzicensis</i> (<i>Plectrohyla</i>) Stuart, 1948	<i>Plectrohyla glandulosa</i>
<i>crassus</i> (<i>Cauphias</i>) Brocchi, 1877	<i>Hyla crassa</i>
<i>crepitans</i> (<i>Hyla</i>) Wied, 1824	<i>Hyla crepitans</i>
<i>crepitans</i> (<i>Acris</i>) Baird, 1854	<i>Acris crepitans</i>
<i>culex</i> (<i>Hyla</i>) Dunn and Emlen, 1932	<i>Hyla staufferi staufferi</i>
<i>curta</i> (<i>Hyla</i>) Cope, 1866	<i>Hyla regilla curta</i>
<i>cyanosticta</i> (<i>Hyla phaeota</i>) Smith, 1953	<i>Smilisca cyanosticta</i>
<i>cyclomaculata</i> (<i>Hyla</i>) Taylor, 1949	<i>Hyla taeniopus</i>
<i>dacnicolor</i> (<i>Phyllomedusa</i>) Cope, 1864	<i>Pachymedusa dacnicolor</i>
<i>dalquesti</i> (<i>Hyla</i>) Taylor, 1949	<i>Hyla taeniopus</i>
<i>darlingi</i> (<i>Hyla</i>) Smith, Smith, and Werler, 1952	<i>Hyla miotympanum</i>
<i>daulinia</i> (<i>Hyla</i>) Cope, 1865	<i>Smilisca baudinii</i>
<i>debilis</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla debilis</i>
<i>dendroscarta</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla dendroscarta</i>
<i>dentata</i> (<i>Pternohyla</i>) Smith, 1957	<i>Pternohyla dentata</i>
<i>deserticola</i> (<i>Hyla regilla</i>) Jameson, <i>et al.</i> , 1966	<i>Hyla regilla hypochondriaca</i>
<i>digueti</i> (<i>Hyliola</i>) Mocquard, 1899	<i>Hyla arenicolor</i>
<i>dolomedes</i> (<i>Hyla baudinii</i>) Barbour, 1923	<i>Smilisca phaeota</i>
<i>duellmani</i> (<i>Hyla</i>) Lynch and Smith, 1966	<i>Hyla chaneque</i>
<i>dulcensis</i> (<i>Hyla</i>) Taylor, 1958	<i>Hyla elaeochroa</i>
<i>ebraccata</i> (<i>Hyla</i>) Cope, 1874	<i>Hyla ebraccata</i>
<i>echinata</i> (<i>Hyla</i>) Duellman, 1962	<i>Hyla echinata</i>
<i>elaeochroa</i> (<i>Hyla</i>) Cope, 1876	<i>Hyla elaeochroa</i>
<i>erythromma</i> (<i>Hyla</i>) Taylor, 1937	<i>Hyla erythromma</i>
<i>euphorbiacea</i> (<i>Hyla</i>) Günther, 1859	<i>Hyla euphorbiacea</i>
<i>euthysanota</i> (<i>Hyla</i>) Kellogg, 1928	<i>Ptychohyla euthysanota euthysanota</i>
<i>eximia</i> (<i>Hyla</i>) Baird, 1854	<i>Hyla eximia</i>
<i>fimbrimembra</i> (<i>Hyla</i>) Taylor, 1948	<i>Hyla fimbrimembra</i>
<i>fodiens</i> (<i>Pternohyla</i>) Boulenger, 1882	<i>Pternohyla fodiens</i>
<i>foliamorta</i> (<i>Hyla</i>) Fouquette, 1958	<i>Hyla rostrata</i>
<i>forbesi</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla arboreoscandens</i>
<i>gabbii</i> (<i>Hyla</i>) Cope, 1876	<i>Smilisca sordida</i>
<i>glandulosa</i> (<i>Hyla</i>) Boulenger, 1883	<i>Plectrohyla glandulosa</i>
<i>godmani</i> (<i>Hyla</i>) Günther, 1901	<i>Hyla godmani</i>
<i>gracilipes</i> (<i>Hyla</i>) Cope, 1865	<i>Hyla eximia</i>
<i>guatemalensis</i> (<i>Plectrohyla</i>) Brocchi, 1877	<i>Plectrohyla guatemalensis</i>
<i>hartwegi</i> (<i>Plectrohyla</i>) Duellman, 1968	<i>Plectrohyla hartwegi</i>
<i>hazelae</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla hazelae</i>
<i>helenae</i> (<i>Agalychnis</i>) Cope, 1885	<i>Agalychnis callidryas</i>
<i>holochroa</i> (<i>Hyla</i>) Salvin, 1860	<i>Agalychnis moreletii</i>
<i>hypochondriaca</i> (<i>Hyla scapularis</i> var.) Hallowell, 1854	<i>Hyla regilla hypochondriaca</i>
<i>ignicolor</i> (<i>Ptychohyla</i>) Duellman, 1961	<i>Ptychohyla ignicolor</i>
<i>immensa</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla miliaria</i>
<i>inflata</i> (<i>Acrodytes</i>) Taylor, 1944	<i>Phrynohyas venulosa</i>
<i>infucata</i> (<i>Hyla pseudopuma</i>) Duellman, 1968	<i>Hyla pseudopuma infucata</i>
<i>ixil</i> (<i>Plectrohyla</i>) Stuart, 1942	<i>Plectrohyla ixil</i>
<i>labeculata</i> (<i>Hyla bistincta</i>) Shannon, 1951	<i>Hyla bistincta</i>

TABLE 1—(Continued)

Trivial name, original generic name, author, and date	Present name
<i>lacertosa</i> (<i>Plectrohyla</i>) Bumzahem and Smith, 1954	<i>Plectrohyla lacertosa</i>
<i>lafrentzi</i> (<i>Hyla</i>) Mertens and Wolterstorff, 1929	<i>Hyla plicata</i>
<i>lancasteri</i> (<i>Hyla</i>) Barbour, 1928	<i>Hyla lancasteri</i>
<i>laticeps</i> (<i>Hyla regilla</i>) Cope, 1889	<i>Hyla regilla curta</i>
<i>latifasciata</i> (<i>Phrynohyas</i>) Duellman, 1956	<i>Phrynohyas venulosa</i>
<i>legleri</i> (<i>Hyla</i>) Taylor, 1958	<i>Hyla legleri</i>
<i>lemur</i> (<i>Phyllomedusa</i>) Boulenger, 1882	<i>Phyllomedusa lemur</i>
<i>leonhardschultzei</i> (<i>Hyla</i>) Ahl, 1934	<i>Ptychohyla leonhardschultzei</i>
<i>lichenosa</i> (<i>Hyla</i>) Günther, 1859	<i>Phrynohyas venulosa</i>
<i>litodryas</i> (<i>Phyllomedusa</i>) Duellman and Trueb, 1967	<i>Agalychnis litodryas</i>
<i>loquax</i> (<i>Hyla</i>) Gaige and Stuart, 1934	<i>Hyla loquax</i>
<i>lythrodes</i> (<i>Hyla</i>) Savage, 1968	<i>Hyla rufoculis</i>
<i>macrotympanum</i> (<i>Hyla</i>) Tanner, 1957	<i>Ptychohyla euthysanota macrotympanum</i>
<i>manisorum</i> (<i>Hyla</i>) Taylor, 1954	<i>Smilisca baudinii</i>
<i>marmorata</i> (<i>Hyla molitor</i> var.) Schmidt, 1857	<i>nomen dubium</i>
<i>martini</i> (<i>Hyla microcephala</i>) Smith, 1951	<i>Hyla microcephala underwoodi</i>
<i>matudai</i> (<i>Plectrohyla</i>) Hartweg, 1941	<i>Plectrohyla matudai</i>
<i>maxima</i> (<i>Rana</i>) Laurenti, 1768	<i>Hyla boans</i>
<i>melanomma</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla melanomma melanomma</i>
<i>microcephala</i> (<i>Hyla</i>) Cope, 1886	<i>Hyla microcephala microcephala</i>
<i>microcephala</i> (<i>Hyla</i>) Boulenger, 1898 (<i>nec</i> Cope)	<i>Hyla microcephala underwoodi</i>
<i>microeximia</i> (<i>Hyla</i>) Maslin, 1957	<i>Hyla eximia</i>
<i>microtis</i> (<i>Hyla</i>) Peters, 1869	<i>Hyla miotympanum</i>
<i>miliarius</i> (<i>Hypsiboas</i>) Cope, 1886	<i>Hyla miliaria</i>
<i>milleri</i> (<i>Hyla</i>) Shamon, 1951	<i>Ptychohyla leonhardschultzei</i>
<i>miotympanum</i> (<i>Hyla</i>) Cope, 1863	<i>Hyla miotympanum</i>
<i>mixe</i> (<i>Hyla</i>) Duellman, 1965	<i>Hyla mixe</i>
<i>mixomaculata</i> (<i>Hyla</i>) Taylor, 1950	<i>Hyla mixomaculata</i>
<i>modesta</i> (<i>Acrodytes</i>) Taylor and Smith, 1945	<i>Phrynohyas venulosa</i>
<i>moesta</i> (<i>Hyla punctariola</i>) Cope, 1876	<i>Hyla pictipes</i>
<i>molitor</i> (<i>Hyla</i>) Schmidt, 1857	<i>nomen dubium</i>
<i>monticola</i> (<i>Hyla punctariola</i>) Cope, 1876	<i>Hyla pictipes</i>
<i>moraviaensis</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla lancasteri</i>
<i>moreletii</i> (<i>Hyla</i>) Duméril, 1853	<i>Agalychnis moreletii</i>
<i>muricolor</i> (<i>Hyla</i>) Cope, 1862	<i>Smilisca baudinii</i>
<i>nana</i> (<i>Hyla</i>) Günther, 1901 (<i>nec</i> Boulenger)	<i>Hyla smithii</i>
<i>nebulosa</i> (<i>Hyla</i>) Hallowell, 1854 (<i>nec</i> Spix)	<i>Hyla cadaverina</i>
<i>nicefori</i> (<i>Gastrotheca</i>) Gaige, 1933	<i>Gastrotheca nicefori</i>
<i>nigripes</i> (<i>Hyla</i>) Cope, 1876	<i>Smilisca sordida</i>
<i>nigropunctata</i> (<i>Hyla</i>) Boulenger, 1882	<i>Phrynohyas venulosa</i>
<i>nubicola</i> (<i>Hyla</i>) Duellman, 1964	<i>Hyla nubicola</i>
<i>oaxaca</i> (<i>Hyla bivocata</i>) Lynch, 1964	<i>nomen nudum</i>
<i>pachyderma</i> (<i>Hyla</i>) Taylor, 1942	<i>Hyla pachyderma</i>
<i>paenulata</i> (<i>Hyla</i>) Brocchi, 1881	<i>Phrynohyas venulosa</i>
<i>panamensis</i> (<i>Cerathyla</i>) Stejneger, 1917	<i>Hemiphractus panamensis</i>
<i>pansosana</i> (<i>Hyla</i>) Brocchi, 1877	<i>Smilisca baudinii</i>
<i>pellita</i> (<i>Hyla</i>) Duellman, 1968	<i>Hyla pellita</i>

TABLE 1—(Continued)

Trivial name, original generic name, author, and date	Present name
<i>pentheter</i> (<i>Hyla</i>) Adler, 1965	<i>Hyla pentheter</i>
<i>petasatus</i> (<i>Pharyngodon</i>) Cope, 1865	<i>Tripriion petasatus</i>
<i>phaeota</i> (<i>Hyla</i>) Cope, 1862	<i>Smilisca phaeota</i>
<i>phantasmagoria</i> (<i>Hyla</i>) Dunn, 1943	<i>Hyla miliaria</i>
<i>phlebodes</i> (<i>Hyla</i>) Stejneger, 1906	<i>Hyla phlebodes</i>
<i>picadoi</i> (<i>Hyla</i>) Dunn, 1937	<i>Hyla picadoi</i>
<i>picta</i> (<i>Hylella</i>) Günther, 1901	<i>Hyla picta</i>
<i>pictipes</i> (<i>Hyla</i>) Cope, 1876	<i>Hyla pictipes</i>
<i>pinorum</i> (<i>Hyla</i>) Taylor, 1937	<i>Hyla pinorum</i>
<i>platycephala</i> (<i>Hylella</i>) Cope, 1879	<i>Hyla sumichrasti</i>
<i>plicata</i> (<i>Hyla</i>) Brocchi, 1877	<i>Hyla plicata</i>
<i>proboscidea</i> (<i>Hyla</i>) Taylor, 1948 (<i>nec</i> Brongersma)	<i>Hyla taeniopus</i>
<i>pseudopuma</i> (<i>Hyla</i>) Günther, 1901	<i>Hyla pseudopuma pseudopuma</i>
<i>pugnax</i> (<i>Hyla</i>) Schmidt, 1857	<i>Hyla crepitans</i>
<i>puma</i> (<i>Hyla</i>) Cope, 1885	<i>Smilisca puma</i>
<i>pynochila</i> (<i>Plectrohyla</i>) Rabb, 1959	<i>Plectrohyla pynochila</i>
<i>quecchi</i> (<i>Plectrohyla</i>) Stuart, 1942	<i>Plectrohyla quecchi</i>
<i>quinquevittata</i> (<i>Hyla</i>) Cope, 1886	<i>Hyla elaeochroa</i>
<i>resinifictrix</i> (<i>Hyla</i>) Goeldi, 1907	<i>Phrynohyas venulosa</i>
<i>reticulata</i> (<i>Diaglena</i>) Taylor, 1942	<i>Tripriion spatulatus reticulatus</i>
<i>richardi</i> (<i>Hyla</i>) Taylor, 1948 (<i>nec</i> Baird)	<i>Hyla fimbrimembra</i>
<i>richardtaylori</i> (<i>Hyla</i>) Taylor, 1954	<i>Hyla fimbrimembra</i>
<i>rickardsi</i> (<i>Hyla</i>) Taylor, 1939	<i>Hyla godmani</i>
<i>rivularis</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla rivularis</i>
<i>robertmertensi</i> (<i>Hyla</i>) Taylor, 1937	<i>Hyla robertmertensi</i>
<i>robertsorum</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla robertsorum</i>
<i>robustofemora</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla crassa</i>
<i>rosenbergi</i> (<i>Hyla</i>) Boulenger, 1898	<i>Hyla rosenbergi</i>
<i>rostrata</i> (<i>Hyla</i>) Peters	<i>Hyla rostrata</i>
<i>rozellae</i> (<i>Hyla</i>) Taylor, 1942	<i>Ptychohyla euthysanota euthysanota</i>
<i>rubra</i> (<i>Hyla</i>) Laurenti, 1768	<i>Hyla rubra</i>
<i>rudis</i> (<i>Hyla</i>) Mocquard, 1899	<i>Pternohyla fodiens</i>
<i>rufiocularis</i> (<i>Hyla</i>) Taylor, 1952	<i>Hyla rufiocularis</i>
<i>rufitela</i> (<i>Hyla</i>) Fouquette, 1961	<i>Hyla rufitela</i>
<i>sagorum</i> (<i>Plectrohyla</i>) Hartweg, 1941	<i>Plectrohyla sagorum</i>
<i>saltator</i> (<i>Agalychnis</i>) Taylor, 1955	<i>Agalychnis saltator</i>
<i>salvadorensis</i> (<i>Hyla</i>) Mertens, 1952	<i>Hyla salvadorensis</i>
<i>salvini</i> (<i>Hyla</i>) Boulenger, 1882	<i>Smilisca sordida</i>
<i>schmidtorum</i> (<i>Ptychohyla</i>) Stuart, 1954	<i>Ptychohyla schmidtorum schmidtorum</i>
<i>sila</i> (<i>Smilisca</i>) Duellman and Trueb, 1966	<i>Smilisca sila</i>
<i>siopela</i> (<i>Hyla</i>) Duellman, 1968	<i>Hyla siopela</i>
<i>smaragdina</i> (<i>Hyla</i>) Taylor, 1940	<i>Hyla smaragdina</i>
<i>smithii</i> (<i>Hyla</i>) Boulenger, 1902	<i>Hyla smithii</i>
<i>sordida</i> (<i>Hyla</i>) Peters, 1863	<i>Smilisca sordida</i>
<i>spatulatus</i> (<i>Tripriion</i>) Günther, 1882	<i>Tripriion spatulatus spatulatus</i>
<i>spilomma</i> (<i>Hyla</i>) Cope, 1877	<i>Phrynohyas venulosa</i>

TABLE 1—(Concluded)

Trivial name, original generic name, author, and date	Present name
<i>spinipollex</i> (<i>Hyla</i>) Schmidt, 1936	<i>Ptychohyla spinipollex</i>
<i>spinosa</i> (<i>Hyla</i>) Steindachner, 1864	<i>Anothea spinosa</i>
<i>splendens</i> (<i>Hyla</i>) Schmidt, 1857	<i>nomen dubium</i>
<i>spurrelli</i> (<i>Agalychnis</i>) Boulenger, 1913	<i>Agalychnis spurrelli</i>
<i>stadelmani</i> (<i>Hyla</i>) Schmidt, 1936	<i>Hyla loquax</i>
<i>staufferi</i> (<i>Hyla</i>) Cope, 1865	<i>Hyla staufferi staufferi</i>
<i>subocularis</i> (<i>Hyla</i>) Dunn, 1934	<i>Hyla subocularis</i>
<i>sumichrasti</i> (<i>Exerodonta</i>) Brocchi, 1879	<i>Hyla sumichrasti</i>
<i>taeniopus</i> (<i>Hyla</i>) Günther, 1901	<i>Hyla taeniopus</i>
<i>taylori</i> (<i>Phyllomedusa callidryas</i>) Funkhouser, 1957	<i>Agalychnis callidryas</i>
<i>thorectes</i> (<i>Hyla</i>) Adler, 1965	<i>Hyla thorectes</i>
<i>thysanota</i> (<i>Hyla</i>) Duellman, 1966	<i>Hyla thysanota</i>
<i>tica</i> (<i>Hyla</i>) Starrett, 1966	<i>Hyla tica</i>
<i>underwoodi</i> (<i>Hyla</i>) Boulenger, 1899	<i>Hyla microcephala underwoodi</i>
<i>uranochroa</i> (<i>Hyla</i>) Cope, 1876	<i>Hyla uranochroa</i>
<i>valancifer</i> (<i>Hyla</i>) Firschein and Smith, 1955	<i>Hyla valancifer</i>
<i>vanvlietii</i> (<i>Hyla</i>) Baird, 1854	<i>Smilisca baudinii</i>
<i>venulosa</i> (<i>Rana</i>) Laurenti, 1768	<i>Phrynohyas venulosa</i>
<i>venusta</i> (<i>Phyllomedusa</i>) Duellman and Trueb, 1967	<i>Phyllomedusa venusta</i>
<i>vermiculata</i> (<i>Hyla</i>) Duméril and Bibron, 1841	<i>Phrynohyas venulosa</i>
<i>vociferans</i> (<i>Hyla</i>) Baird, 1859	<i>Smilisca baudinii</i>
<i>walkeri</i> (<i>Hyla</i>) Stuart, 1954	<i>Hyla walkeri</i>
<i>wellmanorum</i> (<i>Hyla</i>) Taylor, 1952	<i>Smilisca puma</i>
<i>weyeræ</i> (<i>Hyla</i>) Taylor, 1954	<i>Hyla ebraccata</i>
<i>wrightorum</i> (<i>Hyla</i>) Taylor, 1939	<i>Hyla eximia</i>
<i>xanthosticta</i> (<i>Hyla</i>) Duellman, 1968	<i>Hyla xanthosticta</i>
<i>zeteki</i> (<i>Hyla</i>) Gaige, 1929	<i>Hyla zeteki</i>
<i>zonata</i> (<i>Hyla</i>) Spix, 1824	<i>Phrynohyas venulosa</i>

I collected at Chinajá and Toocog in the Departamento El Petén, Guatemala. John Wellman and I returned there in June 1960, and then spent July concentrating our efforts on *Plectrohyla* and *Ptychohyla* in the Guatemalan highlands. In August we were joined by Dale L. Hoyt and spent a month working in the mountains of Chiapas and Oaxaca in México.

In February, 1961, Jerome B. Tulecke and I collected briefly in Guatemala, Honduras, and on Cerro Montecristo in El Salvador, before setting up headquarters in San José, Costa Rica. We spent five months gathering data on Costa Rican hylids and were joined in June by Craig E. Nelson. In July and August, 1961, the three of us worked slowly northward through Central America and México. In the summer of 1962, I was ac-

companied by a group of graduate students to México; we worked briefly in the Sierra Madre Oriental and then spent two months in the Yucatán Peninsula, where we were fortunate to find *Tripurion petasatus* in abundance.

The summer of 1963 was spent in Panamá, accompanied by Charles W. Myers. Studies on hylids were made at Barro Colorado Island and at Achioté on the Caribbean lowlands of Colón Province. Excellent collections were obtained at El Valle, on Cerro La Campana, at Volcán and Boquete in Chiriquí Province, and in the savanna country near Chepo. Through the cooperation of the Gorgas Memorial Laboratory in Panamá, we were able to accompany an expedition to the Serranía del Darién on the Colombian border; there we obtained much valuable material.

In January, 1964, Charles J. Cole and I arrived in Panamá to join Alexander Wetmore and Charles O. Handley, Jr. in another expedition to the Serranía del Darién; our principal objective was Cerro Tacarcuna, the highest mountain in eastern Panamá. The Canal Zone "crisis" disrupted our plans and resulted in our working briefly on Barro Colorado Island and in the Altos de Pacora. The ridges leading to the top of Cerro Tacarcuna still remain untrodden by a herpetologist.

In June of 1964, I again went to México accompanied by a group of graduate students. We worked in the Sierra Madre del Sur in Guerrero and Oaxaca and in the Sierra de Juárez in northern Oaxaca. In early July, I worked briefly in Nicaragua with a field party from the University of Kansas; three of the members of the party—Charles J. Cole, Laurence M. Hardy, and Richard L. Holland—spent most of the summer working in Nicaragua. I went on to Costa Rica and joined Linda Trueb; we collected out of San Isidro el General and Puerto Viejo. Cole and Holland joined us in late August and made collections at Tilarán and Pandora.

In July, 1964, Charles W. Myers initiated three years of field work in Panamá. During the tenure of his stay in Panamá, he sampled the herpetofauna of every part of the country. In February and March, 1965, I joined him for field work in the Bocas Archipelago and in the mountains of Chiriquí. In the summer of 1965, Linda Trueb and I joined Myers for a month in the upper Tuira Basin in Darién, where we discovered *Agalychnis litodryas* and *Phyllomedusa venusta*. In August of the same year, Trueb and I obtained some hylid material from the Golfo Dulce region in Costa Rica.

In early 1966, field work was planned for concentrated effort in areas that were poorly known and to acquire needed recordings and data on life histories. Linda Trueb and I departed in a camper for Middle America in early February, 1966. We spent a week in the cloud forests of eastern México and then worked for a week in the Sierra Madre del

Sur in Oaxaca, where we discovered *Hyla altipotens* and *pellita*. In the highlands of Chiapas, we were unsuccessful in obtaining the rare *Plectrohyla pycnochila*, so we continued into Guatemala and crossed to the north slopes of the Sierra de Cuchumatanes only to be disappointed in finding most of the area heavily cut over and nothing of interest in hylid frogs. As guests of the Escuela Agrícola Panamericana in El Zamorano, Honduras, we spent four unsuccessful days in the cloud forest on Cerro Uyuca. By late March, we were in Costa Rica, where we obtained valuable data at Tapantí, Cinchona, and on the south slope of Cerro de la Muerte. In five days on Volcán Barba, we managed to obtain tadpoles, juveniles, adults, and recordings of the mating call of the rare *Hyla angustilineata*.

Late in April of 1966, we joined Charles W. Myers for a five-week trip from Santa Clara, Chiriquí Province, Panamá, over Cerro Pando, and down to the Río Changuena in Bocas del Toro Province. At each of our four camps, we obtained excellent collections of, and a wealth of data on, hylid frogs. Part of June was spent on the Panamanian savannas and in the Azuero Peninsula before returning to Costa Rica, where, accompanied by Juan R. León and John D. Lynch, we again visited Volcán Barba and Cinchona and spent a profitable four days at Puerto Viejo. Early in July, we met Arthur C. Echternacht in Managua, Nicaragua, and worked briefly in the Sébaco-Matagalpa area before going on to Honduras for a successful assault on Cerro Uyuca for *Hyla salvadorensis*. A brief stay in Guatemala was made memorable by missing a topotypic *Plectrohyla avia*. The first half of August was spent in Oaxaca, where valuable data were obtained in the Sierra Madre del Sur, in the Sierra de Juárez, and on Cerro San Felipe. In the latter part of August, we worked northward through western México. Thus, upon crossing the Río Grande on August 26, 1966, I completed my field work on Middle American hylids, which had begun 15 years before and had amounted to nearly four years in the field.

CLASSIFICATION AND IDENTIFICATION

CLASSIFICATION OF THE HYLIDAE

Approximately 450 species are recognized in the family Hylidae. The variety of morphological, developmental, and behavioral traits of this vast array of species creates some intriguing problems of classification. Two-thirds of the recognized species are currently placed in the genus *Hyla*, which most likely is composite. This genus presently contains such widely divergent Neotropical species as *miiliaria* and *nana* and Australian species as *caerulea* and *ewingi*. In addition to the genus *Hyla*, the other 150 species are placed in 31 genera, some of which are only weakly differentiated from some species groups of *Hyla*, whereas others possess distinctive combinations of characters. Obviously, until a thorough study has been made on the morphology and life histories of at least representatives of all of the genera and of the species groups in *Hyla*, any classification of the hylid frogs is likely to be tenuous. Nevertheless, I am presenting here a tentative classification of the Hylidae with the full realization that many parts of it will not withstand the test of time. Although this classification has many weaknesses, I think it is more realistic than previous ones. Some of the evidence for the classification, together with some of its inherent problems are discussed following its presentation.

FAMILY HYLIDAE HALLOWELL

Hylidae Hallowell, 1857, p. 237.

Frogs having procoelous vertebrae, a double coccygeal condyle, arciferal pectoral girdle, disc-shaped intercalary cartilages between terminal and penultimate phalanges, and usually claw-shaped terminal phalanges.

Subfamily Phyllomedusinae Günther

Phyllomedusidae Günther, 1859, p. 120.

Phyllomedusinae Miranda-Ribeiro, 1926, p. 100.

Frogs having moderately ossified skulls, with or without the dermis co-ossified with the skull; pupil vertical; aquatic tadpoles. Three genera.

Agalychnis Cope, 1864, p. 181. Eight species in Middle America and northwestern South America.

Pachymedusa Duellman, 1968b, p. 5. One species in western México.

Phyllomedusa Wagler, 1830, p. 201. Thirty-one species in tropical America.

Subfamily Hemiphractinae Gadow

Hemiphractinae Gadow, 1901, p. 210.

Frogs having a triangular helmet but without dermis co-ossified with the skull; pterygoids and palatines massive, the latter bearing teeth; pupil horizontal; young developing directly from eggs carried on the back of female. One genus.

Genus *Hemiphractus* Wagler, 1830, p. 743. Five species in northwestern South America and lower Central America.

Subfamily Amphignathodontinae Boulenger

Amphignathodontidae Boulenger, 1882a, p. 449.

Amphignathodontinae Gadow, 1901, p. 139.

Frogs having extensively ossified skulls, with or without the dermis co-ossified with the skull; pupil horizontal; eggs carried on back or in dorsal pouch of females (except *Anothea* and *Nyctimantis*). Eight genera.

Amphignathodon Boulenger, 1882a, p. 450. One species in Ecuador.

Anothea Smith, 1939, p. 190. One species in Middle America.

Cryptobatrachus Ruthven, 1916, p. 1. Two species in the highlands of Colombia.

Flectonotus Miranda-Ribeiro, 1920b, p. 321. One species in southeastern Brasil and one in Venezuela.

Fritziana Mello Leitão, 1937, p. 330. Two species in southeastern Brasil.

Gastrotheca Fitzinger, 1843, p. 30. Nineteen species in southeastern Brasil and the Andes of Bolivia northward into lower Central America.

Nyctimantis Boulenger, 1882a, p. 421. One species in Amazonian Ecuador.

Stefania Rivero, 1967, p. 142. Four species in the Guiana highlands of Venezuela and Guyana.

Subfamily Hyliinae Gray

Hylina Gray, 1825, p. 213.

Hylinae Gadow, 1901, p. 139.

Frogs having variable cranial conditions; pupil horizontal, except in *Nyctimystes*; aquatic tadpoles. Twenty genera.

Acris Duméril and Bibron, 1841, p. 506. Two species in eastern and central North America.

Allophryne Gaige, 1926, p. 1. One species in northeastern South America.

Aparasphenodon Miranda-Ribeiro, 1920a, p. 87. Two species in southeastern Brasil and Orinoco Basin in Venezuela.

Aplastodiscus Lutz, 1950a, p. 612. One species in southeastern Brasil.

Argenteohyla Trueb, 1970b, p. 255. One species in Uruguay and northern Argentina.

Corythomantis Boulenger, 1896, p. 405. One species in northeastern Brasil.

Hyla Laurenti, 1768, p. 32. At least 300 species in all temperate and tropical parts of the world, except Africa from the Sahara southward and the islands in the Pacific Ocean.

Limnaeodius Mittleman and List, 1953, p. 83. One species in southeastern United States.

Nyctimystes Stejneger, 1916, p. 85. Twenty species in New Guinea and northern Australia.

Osteocephalus Steindachner, 1862, p. 77. Five species in Amazonian South America.

Phrynohyas Fitzinger, 1843, p. 30. Six species in tropical America.

Phyllodytes Wagler, 1830, p. 202. Three species in eastern Brasil and one on Trinidad.

Plectrohyla Brocchi, 1877a, p. 93. Ten species in the highlands of northern Central America.

Pseudacris Fitzinger, 1843, p. 31. Seven species in North America east of the Rocky Mountains.

Pternohyla Boulenger, 1882b, p. 326. Two species in western México.

Ptychohyla Taylor, 1944a, p. 41. Five species in the highlands of southern México and northern Central America.

Smilisca Cope, 1865b, p. 194. Six species

in Middle America and northwestern South America.

Sphaenorhynchus Tschudi, 1838, p. 71. Seven species in tropical South America east of the Andes.

Trachycephalus Tschudi, 1838, p. 74. Three species in eastern South America and Pacific lowlands of Ecuador and Colombia.

Triprrion Cope, 1866a, p. 127. Two species in western México and Yucatan Peninsula.

The arrangement given here differs from Goin's (1961b) synopsis of hylid genera by the addition of four genera (*Stefania* Rivero, 1967, *Pachymedusa* Duellman, 1968b, *Argenteohyla* Trueb, 1970b, and *Limnaeodius* Mittleman and List, 1953; the latter was placed as a synonym of *Hyla* by Goin 1961b) and the deletion of six genera. Trueb (1970a) synonymized *Diaglena* with *Triprrion* and *Tetraprrion* with *Trachycephalus*. Bokermann (1966b) treated *Nototheca* as a synonym of *Flectonotus*; *Habrahyla* Goin (1961a) is a synonym of the rhacophorid *Leptopelis* Günther, 1859 (Mertens, 1963). *Cerathyla* is synonymized with *Hemiphractus* in this paper, and *Hyloscirtus* is synonymized with *Hyla*. Bokermann (1966a) showed that *Phyllodytes* Wagler, 1830, is an earlier name for *Amphodius* Peters, 1872.

The subfamilial arrangement given here is based on seemingly minor morphological characters and on life history. The status of the Neotropical genera in the Phyllomedusinae was discussed by Duellman (1968b), who gave considerable weight to the presence of a vertical pupil in those genera. In the advanced families of frogs, vertical pupils occur sporadically in some African ranids and rhacophorids and consistently in the phyllomedusine hylids and some primitive Australian leptodactylids. *Triprrion* and *Nyctimantis* have horizontal pupils; some earlier workers reported vertical pupils in those genera. Lynch (1969) considered the condition of the pupil in leptodactylids as an indication of relationships with the megophryine pelobatids.

All of the phyllomedusine genera have a differentiation of an anterior slip of the submaxillaris muscle, a condition so far known to occur only in some of the Australian species currently placed in the genus *Hyla*. *Cei*

(1963) and Cei and Ersamer (1966) noted the distinctive biochemical properties of the skin in Neotropical phyllomedusines; the results of their current researches on some of the Australo-Papuan hylids should be interesting with regard to the relationships of *Nyctimystes* to the American genera.

With the exception of *Anotheca* and *Nyctimantis*, in all of the amphignathodontine genera the females carry the eggs on their backs (*Cryptobatrachus*, *Fritziana*, and *Stefania*) or in a dorsal pouch (*Amphignathodon*, *Flectonotus*, and *Gastrotheca*). The relationships of these genera are indicated by the nature of the brooding habits and varying stages of the development of a brood pouch from the simple adherence of eggs on the back in *Stefania* to the individual depressions for eggs in *Cryptobatrachus* and a single large basin with individual depressions in *Fritziana*. A slit-like dorsal pouch is present in *Flectonotus*; only the posterior end of the slit is open as a puckered aperture in *Gastrotheca*, and *Amphignathodon*. These two genera seem to be closely related and perhaps should be placed in one genus. *Amphignathodon* differs from all other hylids by having teeth on the dentary. Nothing is known about the life history of *Nyctimantis*. *Anotheca* differs from all other amphignathodontine genera by having much less specialized breeding habits; the eggs are deposited and the tadpoles develop in arboreal bromeliads or water-filled cavities in trees. However, on the bases of general cranial characters and features of external morphology, *Anotheca* closely resembles the casque-headed species of *Gastrotheca*. Thus, mindful that these similarities may be the result of convergence, I tentatively place *Anotheca* in the Amphignathodontinae rather than the Hyalinae.

Hemiphractus is a morphological oddity. The peculiar skull is mostly due to modifications of the dermal roofing bones. The presence of odontoids on the prevomers and dentaries is unique among hylids. The eggs are carried in separate depressions on the backs of females and hatch into frogs. Despite the similarities in brooding and development, I consider the morphological modifications to be of sufficient magnitude to set *Hemiphractus* apart as a separate subfamily from the Amphignathodontinae.

The remaining 19 genera are placed in the Hyalinae. Although there is excellent evidence in support of relationships among some groups of genera in the subfamily, there is little evidence of relationships between some other genera. Thus, the Hyalinae is composed of all those genera that cannot be relegated to some other subfamily. The greatest need for research is with the frogs in this subfamily.

I have not recognized the subfamily Triprioninae Miranda-Ribeiro, 1926; Trueb (1970a) showed that the casque-headed genera assigned to this subfamily represent at least three phyletic lines from *Hyla*. Thus, *Smilisca*, *Pternohyla*, and *Triprion* are closely related, and *Phrynohyas*, *Argenteohyla*, *Osteocephalus*, and *Trachycephalus* represent a single phyletic line (Trueb, 1970b). *Corythomantis* and *Aparasphenodon* apparently have diverged from a *Hyla rubra* group stock. *Acris*, *Limnaeodius*, and *Pseudacris* seem to form a closely related group of genera in North America. *Plectrohyla* and *Ptychohyla* are independently derived groups from Middle American *Hyla*. *Sphaenorhynchus* and *Phyllodytes* apparently are South American derivatives of *Hyla*. The status of the monotypic South American *Aplastodiscus* and *Allophryne* is questionable. Lynch and Freeman (1966) noted the T-shaped terminal phalanges and absence of teeth in *Allophryne* and tentatively referred *Allophryne ruthveni* to the Hylidae.

The clues to the relationships of many of the genera of hyline frogs are hidden in the complexities of the immense genus *Hyla*. Obviously, the frogs currently placed in this genus have undergone a tremendous adaptive radiation, which through divergence, convergence, and parallelism has resulted in an obfuscation of relationships. A major problem is the possible polyphyletic nature of the genus *Hyla* as now recognized. The similarities in vertebral characters and the identical number of chromosomes in some of the Australian *Hyla* with *Nyctimystes* and the Neotropical phyllomedusines perhaps is evidence for closer relationships of those Australian *Hyla* with the phyllomedusines than with the hylines.

I have few illusions to the permanence of these ideas. My intention in presenting the classification and the feeble amount of evi-

dence in support of the arrangement has not been to provide a fixed classification but rather to stimulate the search for new evidence so that in the future a realistic classification of hylid frogs will be based on an amalgamation of morphological, developmental, behavioral, biochemical, and cytogenetic evidence.

TAXONOMIC CHARACTERS AND CRITERIA IN HYLID FROGS

Proper assessment of the morphological and behavioral traits of the Middle American hylid frogs is dependent upon an understanding of the kinds of characters and the nature of the variation in these characters. Each of the characters used in the taxonomic study of the Middle American hylids is defined and discussed in the following paragraphs. Adaptive significance, evolutionary trends, and relationships between morphological characters and environmental conditions are excluded here. They are presented in the later discussions of relationships and distribution.

EXTERNAL MORPHOLOGY

Among the herpetological forms of life, frogs are notorious for their lack of definitive external characters. The absence of scales, costal grooves, or other countable characters is faced by most workers with mixed feelings. To someone like myself, who counted tens of thousands of scales on *Leptodeira* and spent countless hours peering through a microscope while counting the granules on *Cnemidophorus*, the absence of such taxonomically important structures in frogs is a great blessing. Although there are some definite "present or absent" external characters in hylids, most of the differences are relative. During a visit to the Academy of Natural Sciences of Philadelphia many years ago, I handed the late Emmett R. Dunn two hylids that he had identified as different species and asked him how he distinguished one from the other. He carefully compared them for a minute and then boldly announced: "They look different. That's how." Upon close examination I, too, could see that they looked different. Perhaps some of my readers will feel that in the accounts of the species I have unduly belabored

certain aspects of the descriptions of external characters. However, I am merely trying to relate what the frogs look like.

Measurements and Proportions

Seven measurements were routinely made (fig. 2): snout-vent length—direct line distance from the tip of the snout (excluding a fleshy proboscis, if present) to the posterior margin of the vent; tibia length—straight length of the tibia; foot length—distance from the proximal edge of the inner metatarsal tubercle (the large tubercle at the base of the first toe) to the tip of the longest (fourth) toe, including disc; head length—straight line distance from the posterior edge of the jaw articulation to the tip of the snout; head width—the greatest width of the head, usually at about the level of the anterior edges of the tympani; diameter of the eye—greatest length of the orbit; diameter of the tympanum—greatest horizontal distance between the outer edges of the tympanic ring. Four other measurements were taken on some species: interorbital distance—the width of the frontoparietals between the orbits; width of eyelid

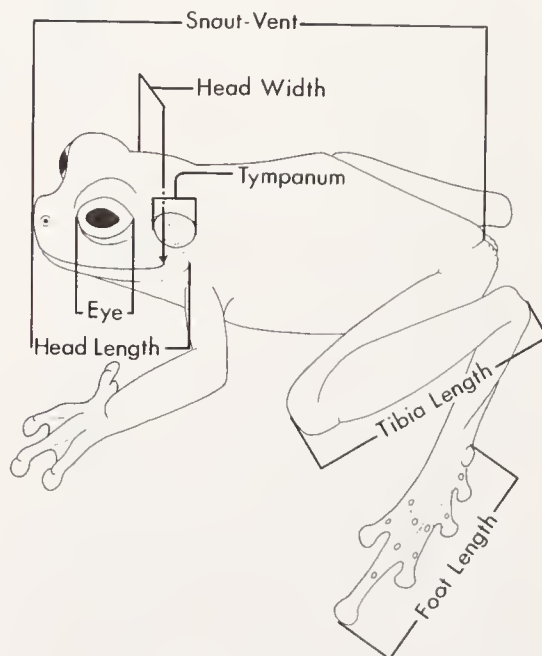


FIG. 2. A hylid frog showing places of measurements.

—greatest width of the upper eyelid; internarial distance—the distance between the median margins of the external nares; snout length—the straight line distance between the anterior corner of the orbital opening and the posterior margin of the external nares.

Measurements of preserved frogs have limited values. Because it can be assumed that frogs continue to grow throughout life and have slight changes in proportions during growth, even after sexual maturity, the usefulness of measurements, except for snout-vent length in adults, is of much less taxonomic value than in endotherms. Because of continued growth, proportions rather than actual measurements, are better for making comparisons between samples and species. On all specimens four ratios to snout-vent length were calculated: tibia length, foot length, head length, and head width. In those species having distinct tympani, the ratio of the diameter of the tympanum to that of the eye was calculated. The interorbital distance, internarial distance, and width of the eyelid are expressed as ratios of the head width, and the snout length is expressed as a ratio of the head length or the diameter of the tympanum.

The size of Middle American hylids varies from that of *Hyla picta*, in which males reach a known maximum snout-vent length of 21.4 mm., to the gigantic *Hyla boans*, in which males attain a maximum snout-vent length of 131.9 mm. Other very small species of *Hyla* and the maximum snout-vent lengths of males are: *subocularis* (23.1 mm.), *zeteki* (23.5 mm.), and *phlebodes* (23.6 mm.). The very large species in which the maximum snout-vent length exceeds 100 mm. in males, besides *Hyla boans*, are *Hyla miliaria* (106.0 mm.) and *Phrynohyas venulosa* (100.5 mm.). The Hispaniolan *Hyla vasta* is usually considered to be the largest hylid frog; Cochran (1941, p. 21) reported a female of that species with a snout-vent length of 142 mm., but her largest male had a snout-vent length of 112 mm., considerably smaller than the largest Panamanian *Hyla boans* and even smaller than the average snout-vent length of 119.9 mm. in ten *Hyla boans* from Salsarí Panamá. Thus, it is likely that *Hyla boans* is the largest species in the family.

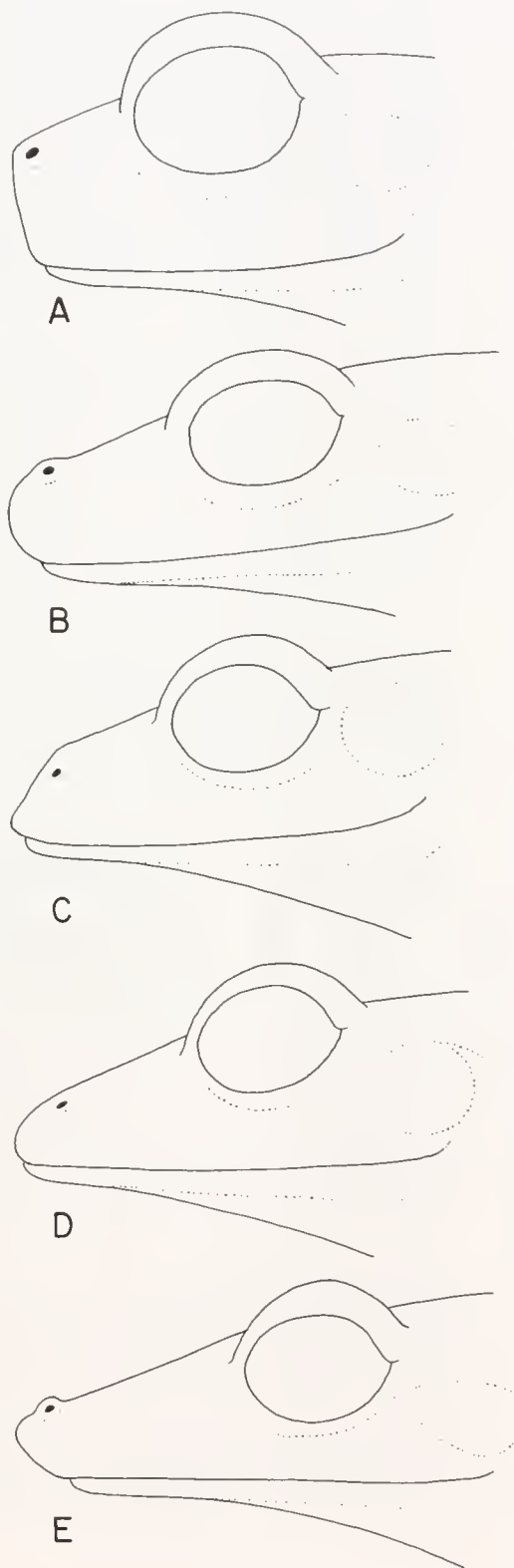
In general terms, I have referred to species in which the males have snout-vent lengths of 30 mm. or less as being small, 30 to 50 mm. as medium-sized, 50 to 80 mm. as large, and more than 80 mm. as very large. Usually the members of a given species group are in the same size-class. For example, all members of the *Hyla microcephala* group are small, and all members of the *Hyla taeniopus* group are large. For the most part, closely related species are similar in size.

The general habitus or shape of the body is difficult to measure and is expressed in general terms. Most hylids, except gravid females, are rather slender frogs. There are two major exceptions—the squat toad-like body of *Pterohyla* and the depressed body of *Hemiphractus*.

Head

The head is generalized in most species, but it is modified in some in which the cranial roofing bones are expanded and frequently co-ossified with the skin (see discussion of dermal modification in section on Cranial Osteology). The development of broad labial flanges and cranial crests results in a highly modified head in *Pterohyla* and *Triprion*. The head of *Anotheca* is modified by the presence of numerous spines arising from the dermal cranial bones, and that of *Hemiphractus* is arrow-shaped due to the posterolateral expansion of the squamosals.

The shape of the snout is a reliable and easily discernible taxonomic feature. In dorsal view, the snout is truncate, round, or acuminate; these same shapes are evident in lateral views, but laterally, the snouts of some species are sloping or acuminate and protruding beyond the margin of the lower jaw, such as in *Hyla boulengeri* (fig. 3). In *Hyla chryses* and *siopela*, *Ptychohyla leonhardschultzei* and *spinipollex*, and *Plectrohyla ixil* and *matudai*, a fleshy vertical rostral keel is present (fig. 4G and H). This keel is readily apparent in most individuals of those species, except specimens that are soft and have been standing on their noses in jars for a number of years. In all juveniles and in most adults of *Hemiphractus panamensis*, a fleshy triangular proboscis is present on the tip of the snout (fig. 4I). The only other dermal appendage



on the head is the fleshy supraorbital "horn" that is well developed in *Gastrotheca ceratophrys* and less so in *Hemiphractus panamensis* (fig. 4I and J).

Three characters on the anterior part of the head are highly subjective; these are the canthus (canthus rostralis), loreal region, and the lips. The canthus is the angle of the head from the anterior corner of the eye to the nostrils or to the tip of the snout. The condition of the canthus varies: indistinct and rounded, distinct and rounded, angular, acutely angular, and elevated and ridge-like. The loreal region is the side of the face between the canthus and the lips. The condition of the loreal region is a reflection of the nature of the canthus and the lips. In most hylids, the loreal region is slightly concave; in a few species it is nearly flat and inclined laterally, and in species with prominent canthal ridges and flared lips, the loreal region is deeply concave. The nature of the lips is most easily determined in an anterior view. In those hylids having robust, but generalized, heads the lips tend to be massive (thick) and barely, if at all, flared laterally. Those species having depressed heads tend to have thin and flared lips. The lateral flaring is most pronounced in the species of *Triprrion*, which have broad labial flanges. The nature of these three facial features is primarily dependent upon the structure of the underlying nasal and pars facialis of the maxillary.

The pupil of the eye is horizontally elliptical in all Middle American hylids, except the phyllomedusine genera *Agalychnis*, *Pachymedusa*, and *Phyllomedusa*, in which it is vertically elliptical (fig. 5). The palpebral membrane, the transparent lower eyelid, is unpigmented or only barely pigmented in most species. However, in *Hyla boans*, *Pachymedusa dacnicolor*, and all species of *Agalychnis* (except *calcarifer*), the membrane has a pigmented reticulation (fig. 5).

A dermal fold, the supratympanic fold, extends posteriorly from the corner of the eye. This fold passes just above the tympanum and continues onto the flank, slopes downward to a point above the insertion of

FIG. 3. Lateral views of heads of hylid frogs showing shapes of snouts. A. Truncate. B. Round. C. Sloping. D. Acuminate. E. Protruding.

the arm, or angles ventrally to the angle of the jaw. In most species, the fold obscures the upper edge of the tympanum, and in some of those in which the fold drops to the angle of the jaw, the posterior edge of the tympanum also is covered. In most of the small species and most pond-breeding hylids the

supratympanic fold is comparatively thin, whereas it is much heavier in some of the larger stream-breeding frogs of the *Hyla* *bistincta* and *taeniopus* groups and in those of the genus *Plectrohyla*. In these frogs, the tympanum in some individuals is nearly hidden beneath the supratympanic fold. The same condition exists in some specimens of *Phrynohyas* (see discussion of parotoid glands in the section on skin). A tympanum and usually a tympanic ring are evident in most Middle American hylids. The tympanum is barely evident and the tympanic ring absent in *Hyla melanomma*, *picadoi*, and *zeteki*. The tympanum is completely concealed beneath the skin in *Plectrohyla lacertosa*, *Hyla pachyderma*, *Hyla pinorum*, and the four species in the *Hyla mixomaculata* group. With the exception of *Hyla picadoi* and *zeteki*, which breed in bromeliads, all species in which the tympanum is indistinct or concealed are stream breeders.

The tongue in hylids is not extensible; it is usually barely free behind and free for no more than half of its length. The shape of the tongue is of some taxonomic importance; however, the shape is dependent upon careful

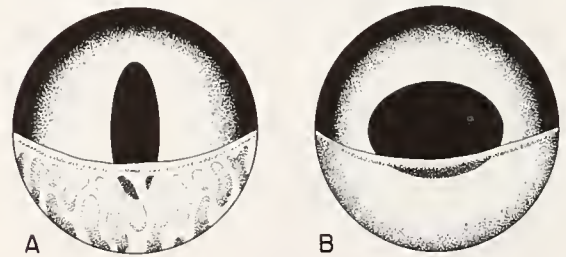
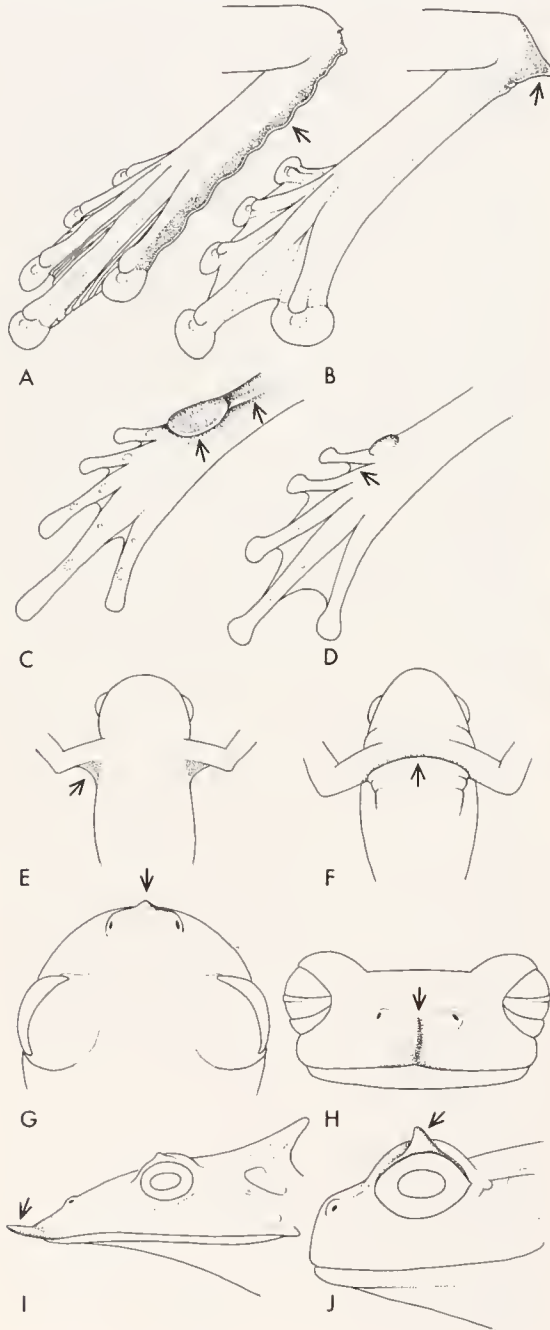


FIG. 5. Eyes of hylid frogs. A. Vertical pupil and reticulated palpebral membrane. B. Horizontal pupil and unpigmented palpebral membrane.

FIG. 4. External morphological characters of hylid frogs. Arrows indicate important structures. A. Foot showing dermal fringe. B. Foot showing calcar. C. Foot of *Pterohyla fodiens* showing spatulate inner metatarsal tubercle and tarsal fold. D. Foot of *Hyla elaeochroa* showing reduced webbing between first and second toes characteristic of the *Hyla rubra* group. E. Axillary membrane. F. Thoracic fold. G and H. Rostral keel. I. Fleshy proboscis on *Hemiphractes panamensis*. J. Supraocular fleshy "horn" on *Gastrotheca ceratophrys*.

and uniform preparation. Four shapes are recognized in Middle American hylids: round, cordiform (heart-shaped), elongately ovoid, and lanceolate (fig. 6). The vocal slits are paired—one on either side of the floor of the mouth. The slit usually extends from the midlateral base of the tongue nearly to the angle of the jaw; in some groups, the slit lies along the median edge of the mandible.

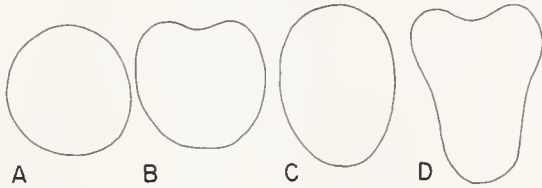


FIG. 6. Tongues of hylid frogs. A. Round. B. Cordiform. C. Ovoid. D. Lanceolate.

The vocal sacs of Middle American hylids are of four structural types (fig. 7). The most common type is the single median subgular sac; in *Hyla pseudopuma*, the sac is weakly constricted medially and is termed a bilobate subgular sac. In *Triprrion petasatus* and all species of *Smilisca* and *Pternohyla* the vocal sac forms two bulbous protrusions with a deep medial constriction between; this type is called the paired subgular vocal sac. In *Phrynohyas*, the vocal sacs are paired and behind the angles of the jaws. The vocal sacs in all of these frogs are formed by modification of the thin submaxillaris (intermandibularis) muscle. The submaxillaris is attached medially by fascia to the deeper hyoglossus and geniohyoideus muscles in those species having paired subgular vocal sacs. The paired lateral sacs in *Phrynohyas* are formed by posterolateral extensions of the submaxillaris (see Duellman, 1956a, for detailed description). The single, median subgular vocal sacs in most of the pond-breeding frogs are greatly distensible, whereas in many of the stream-breeding species, the sacs are only moderately or barely distensible. Vocal slits, vocal sac, and presumably a voice are lacking in *Hyla altipotens*, the *Hyla bistincta* group (except *bistincta* and *peniheter*), the *Hyla mixomaculata* group, the large species of *Plectrohyla*, and in some populations of *Hyla chaneque*.

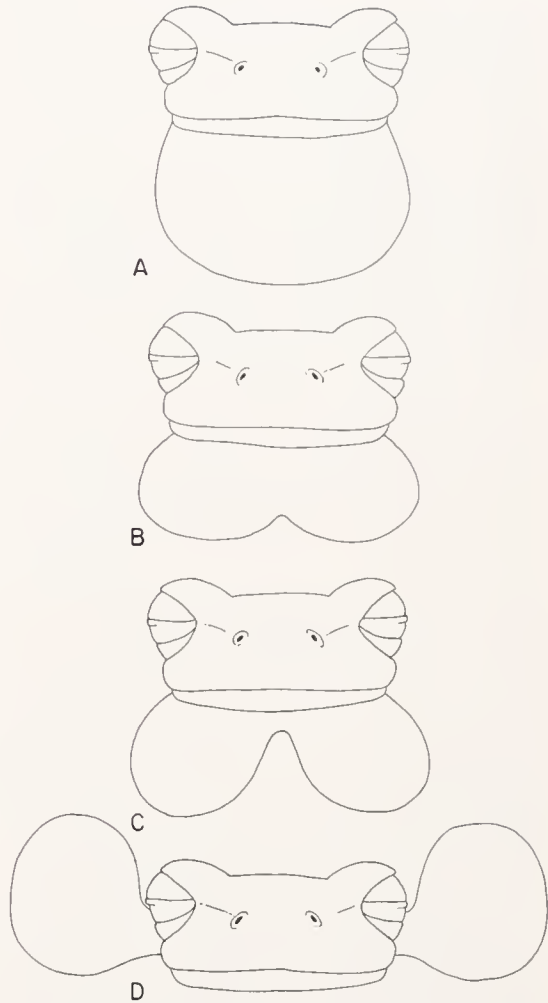


FIG. 7. Structural types of vocal sacs. A. Single, median, subgular. B. Bilobate subgular. C. Paired subgular. D. Paired lateral.

Skin

The nature of the skin, its structure and modifications in such places as around the anal opening, the presence of dermal appendages, and the kinds and positions of glands, are of considerable taxonomic importance. It must be noted however that the nature of the dermal features is strongly affected by preservation. Generally in specimens that are soft and poorly preserved or in those that were slightly decomposed prior to preservation, rugosities, folds, and tubercles are minimized, whereas in specimens that have been desiccated or preserved in very

strong formalin, those structures are emphasized. In general, the skin on the dorsum of most hylids is smooth; that on the ventral surfaces of the arms and shanks is smooth and that on the throat, chest, belly, and ventral surfaces of the thighs is granular. The granules are not apparent in the skin of distended vocal sacs. The skin on the dorsum in several species of *Hyla* and some of *Plectrohyla* is weakly tuberculate and that in *Phrynohyla* is strongly tuberculate. In the populations of *Hyla lancasteri* at high elevations, the tubercles are elongated into fleshy "spines."

In some species in the *Hyla bistincta*, *parviceps*, *rivularis*, and *taeniopus* groups, a thoracic fold (fig. 4F) is present. This should not be confused with the transverse dermal fold formed by the deflated vocal sac in breeding males. A web of skin, an axillary membrane (fig. 4E), extends from the flank to the posterior edge of the forearm. This membrane extends nearly to the elbow in members of the *Hyla godmani* and *sumichrasti* groups and is less extensive but present in all members of the *bromeliacia*, *erythromma*, *microcephala*, *mixomaculata*, *picta*, and *rivularis* groups of *Hyla*. An axillary membrane is present in the three small members of the *Hyla rubra* group and in some members of the *Hyla bistincta* group.

A row of tubercles is present on the ventrolateral edge of the forearm in many species; these are most prominent in some of the larger stream-breeding frogs, such as members of the *Hyla bistincta* and *taeniopus* groups. In most Middle American hylids, a transverse dermal fold is present on the dorsal surface of the wrist and the outer surface of the heel. Members of the *Hyla miliaria* group have a scalloped dermal fringe along the outer edges of the forearms, hands, and feet (fig. 4A); these are the so-called fringe-limbed hylids. A prominent triangular dermal flap or calcar is present on the heel in *Agalychnis calcarifer*, *Gastrotheca ceratophrys*, *Hemiphractus panamensis*, and *Hyla boans* (fig. 4B).

The position of the anal opening and its attendant folds and tubercles show various modifications in Middle American hylids. In most of the small pond-breeding frogs, the anal opening is directed posteriorly at the up-

per level of the thighs and is covered by a short, broad anal flap (fig. 8A). In some pond-breeders and many stream-breeding hylids, the anal opening is directed posteroventrally at the midlevel of the thighs and covered by a moderately long anal sheath (fig. 8B). The anal opening is directed ventrally near the ventral surfaces of the thighs and covered by an elongate anal sheath in some *Agalychnis*, *Pachymedusa dacnicolor*, and some members of the *Hyla bistincta* and *taeniopus* groups (fig. 8C). The only dorsal aperture is the brood pouch in females of *Gastrotheca*. Females of *Hemiphractus* that are carrying eggs or young have depressions in the dorsal skin; the eggs and at later stages, the young are attached to the skin in these depressions (pl. 7).

The skin in hylids contains numerous mucous glands and fewer poison glands; the latter apparently are modified mucous glands. Poison glands are concentrated in the extensive parotoid glands in *Phrynohyla*, in which the skin is thickened and glandular on the head and neck. McDiarmid (1968, p. 20) demonstrated that the parotoid glands are better developed in specimens obtained in

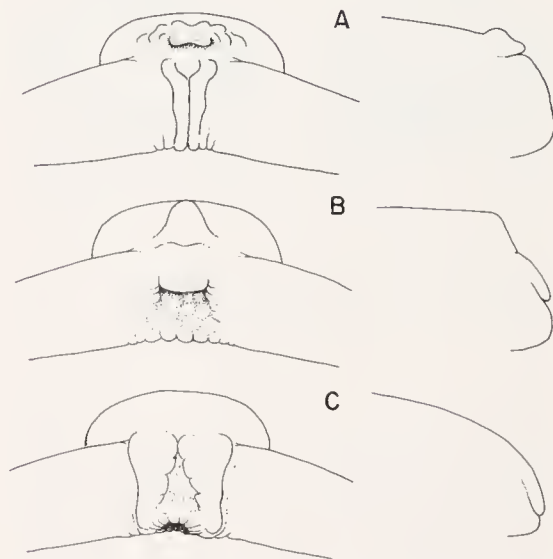


FIG. 8. Posterior and sectional views of anal openings. A. Directed posteriorly at upper level of thighs. B. Directed posteroventrally at midlevel of thighs. C. Directed ventrally at lower level of thighs.

the dry season than in those collected in the rainy season. Because of the slime secretion by these frogs and the effectiveness of the slime in preventing desiccation, McDiarmid suggested that "the greater development and subsequent secretion of the glands in the dry season is produced as an adaptive response to arid environments." Long, elevated dorsolateral parotoid glands are present in *Phyllomedusa venusta*.

Breeding males of the genus *Ptychohyla* have thickened, pigmented ventrolateral glands on the body (fig. 9A). The glandular areas seem to be composed of large concentrations of mucous glands. Because the glands are present only in breeding males, it is surmised that the glands are associated with some phase of the breeding activity. Adults of both sexes of *Hyla colymba* have an ovoid "mental gland" on the chin (fig. 9B); the histological structure and function of the gland is unknown.

Osteoderms are present in the dorsal skin of *Hyla miliaria* and *Phyllomedusa venusta*. Possibly these result in a decrease in the permeability of the skin and help to reduce desiccation in these arboreal frogs. The tips of granules on the chest in some specimens of *Smilisca phaeota* and on various parts of

the venter in large specimens of *Hyla miliaria* are keratinized. The significance of keratinization of the granules is unknown.

Hands and Feet

The structural characters of the hands and feet are of immense taxonomic importance and are easily studied on specimens that have been fixed in trays with their hands and feet spread and the digits straight. The terminology of the structures of the hands and feet is as follows:

Digit: any one of the four fingers or five toes.

Phalanx: any one of the bony segments of a given digit; the terminal phalanx (disc) is offset ventrally and separated from the proximally adjacent phalanx by an intercalary cartilage.

Disc: the terminal phalanx; it is expanded and flattened in most species.

Penultimate phalanx: the phalanx immediately proximal to the disc.

Antepenultimate phalanx: the phalanx immediately proximal to the penultimate phalanx.

Thumb: the first (inner) digit on the hand.

Prepollex: the vestigial digit on the inner base of the thumb.

Prepollical spine: the bone supporting the prepollex and protruding through the distal end of the prepollex in some species.

Nuptial excrescence: the horny pad or keratinized area on the inner surface of the prepollex (also on other digits in some species) in breeding males.

Subarticular tubercles: those tubercles below the articulations of the phalanges.

Supernumerary tubercles: the small tubercles on the ventral surfaces of the digits, exclusive of the larger subarticular tubercles; absent in some hylids.

Palmer tubercle: one or more tubercles on the palm at the bases of the third and fourth fingers.

Inner metatarsal tubercle: the large tubercle on the ventral surface of the foot at the base of the first (shortest) toe (fig. 4C).

Outer metatarsal tubercle: a small tubercle on the ventral surface of the foot at the base of the fourth (longest) toe; absent in many species.

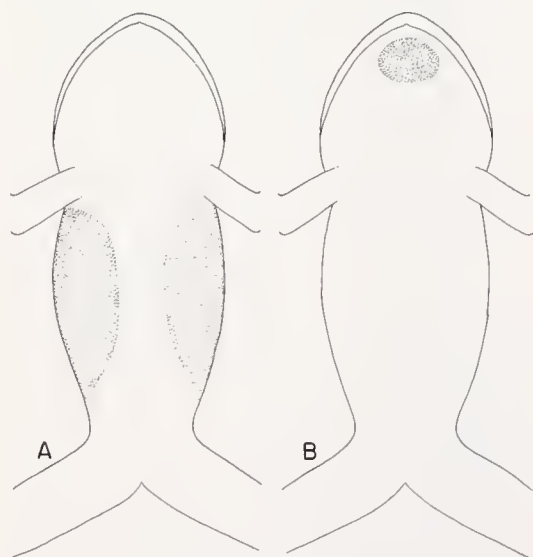


FIG. 9. Glands on ventral surfaces. A. Ventrolateral glands of *Ptychohyla*. B. Mental gland of *Hyla colymba*.

Tarsal fold: a dermal fold on the ventral surface of the foot commencing at the heel or distal thereto and terminating at the inner metatarsal tubercle (fig. 4C).

Outer tarsal fold: a weak dermal fold on the outer edge of the foot in some populations of *Ptychohyla glandulosa*.

Web: the membranous skin connecting the fingers and the toes.

The relative lengths of the digits, from shortest to longest, are on the hand 1-2-4-3 and on the foot, 1-2-5-3-4. The relative lengths of the fingers differs in *Hemiphractus* and *Gastrotheca*; in those genera the first finger (thumb) is longer than the second. In *Phyllomedusa venusta* the first toe is longer than, and opposable to, the second. The fingers are proportionately longer in *Gastrotheca*, *Anotheca*, *Hemiphractus*, and the stream-breeding frogs of the *Hyla bistincta*, *lancasteri*, and *pictipes* groups and *Plectrohyla*. The fingers are proportionately shorter in many of the pond-breeding frogs, such as *Agalychnis* and members of the *Hyla godmani*, *leucophyllata*, *microcephala*, and *picta* groups. Short fingers are characteristic of the bromeliad-breeding members of the *Hyla bromeliacia* group and the stream-breeding *Hyla sumichrasti* group. The terminal discs on the fingers are usually larger than those on the toes. The discs are round, or nearly so, in all species except *Hyla boulengeri* and *rostrata*, in which they are truncate. The terminal phalanges are not expanded in *Acris*, *Hemiphractus*, *Pternohyla*, and *Phyllomedusa venusta* and barely expanded in *Pseudacris* and members of the *Hyla eximia* group. In most of the large arboreal hylids, the discs are proportionately very large, such as in *Agalychnis*, *Anotheca*, *Gastrotheca*, *Phrynohyas*, and members of the *Hyla albomarginata*, *boans*, and *miliaria* groups. Large discs are also present in the three largest species of *Plectrohyla* (*avia*, *guatemalensis*, and *hartwegi*).

The subarticular tubercles vary in size and structure. They are largest in some of the large arboreal groups, such as *Agalychnis*, *Gastrotheca*, *Phrynohyas*, and the *Hyla albomarginata*, *boans*, and *miliaria* groups. The subarticular tubercles also are large in the

terrestrial *Pternohyla* and the stream-breeding *Plectrohyla* and members of the *Hyla bistincta* and *taeniopus* groups. The subarticular tubercles usually are round or subconical, but in many species, the distal tubercle on the fourth finger (and in some individuals, the distal tubercle on the third finger) is bifid or even divided (fig. 10). Bifid subarticular tubercles are characteristic of such diverse groups as *Phrynohyas*, *Plectrohyla*, *Ptychohyla*, *Hemiphractus*, and in the *Hyla leucophyllata*, *microcephala*, and *rivularis* groups; bifid tubercles occur in many other groups. Because of the variability of the distal subarticular tubercle on the fourth finger, I do not consider the bifid versus entire tubercle to be of much taxonomic importance.

The shape of the prepollex, the presence or absence of a nuptial excrescence, and the kind of nuptial excrescence are important taxonomic characters of the thumb. Most species having an enlarged prepollex also have a nuptial excrescence, which is a smooth horny covering or composed of minute spinules (fig. 11B). The excrescence is made up of a cluster of large spines in members of the *Ptychohyla cuthysanota* group, *Hyla echinata*, *Hyla pachyderma*, and highland populations of *Hyla lancasteri* (fig. 11C). In *Hyla zeteki*, the prepollex is greatly enlarged and bulbous (fig. 11A), and in *Hyla valancifer* it is enlarged and spatulate; in both species a nuptial excrescence is absent. In *Plectrohyla*, *Hyla miliaria*, and members of the *Hyla albomarginata* and *boans* groups, the prepollex is greatly enlarged and is supported by a prepollical spine, which protrudes through the distal end of the prepollex in

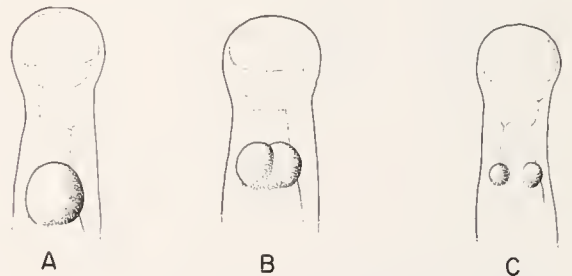


FIG. 10. Distal subarticular tubercles on fourth fingers. A. Normal, round. B. Bifid. C. Divided.

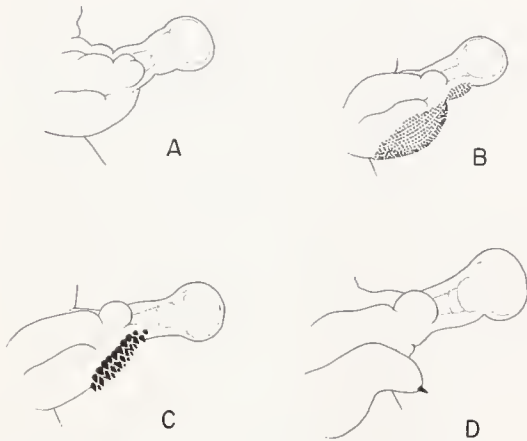


FIG. 11. Ventral views of right prepollices showing nuptial conditions in males. A. *Hyla zeteki*, enlarged and lacking nuptial excrescence. B. *Hyla robertsoni*, enlarged and having a generalized nuptial excrescence. C. *Ptychohyla spinipollex* with a cluster of nuptial spines. D. *Hyla crepitans* with elongately enlarged prepollex and protruding prepollical spine.

some individuals (fig. 11D). The shape of the prepollical spine is an important taxonomic character in *Plectrohyla* (see account of that genus). In addition to those groups just mentioned, several others lack nuptial excrescences on relatively unenlarged prepollices—*Acris*, *Anotheca*, *Hemiphraactus*, *Ptychohyla schmidtorum* group, and members of the *Hyla colymba*, *godmani*, *leucophyllata*, *microcephala*, *mixomaculata*, and *rubra* groups.

An inner metatarsal tubercle is present in all species of Middle American frogs. The tubercle varies in size and shape from elongately elliptical to ovoid; in *Pternohyla fodiens*, the edge of the tubercle is elevated and spatulate (fig. 4C). The outer metatarsal tubercle is small or absent in all species.

Most students of hylid taxonomy have given considerable taxonomic weight to the presence or absence of a tarsal fold on the inner edge of the tarsus (fig. 4C). In many species, the fold is strong and flap-like; in others it is weak or absent. The status of the tarsal fold in many small species having weak folds is difficult to determine. In specimens that have been fixed in trays with the plantar surface down, the fold is obscured. Thus, in many individuals, it is not possible to determine if a tarsal fold is present. A weak outer

tarsal fold is present in some populations of *Plectrohyla glandulosa*.

The extent of the webbing on the hands and feet shows a vast amount of interspecific variation. The feet are fully webbed and the hands nearly fully webbed in *Agalychnis litodryas* and *spurrelli* and in *Hyla boans*, *crassa*, *mixe*, *nubicola*, *echinata*, *miliaria*, and *thysanota*. Webbing is absent, or nearly so, on the hands and feet of *Pseudacris*, *Pternohyla*, *Phyllomedusa*, and *Hemiphraactus*. Webbing is essentially absent on the hands of *Acris*, *Anotheca*, *Gastrotheca*, and some species of *Hyla*, but in these the toes are webbed. In the accounts of the species, the amount of webbing is expressed in general and in detail. The general terms of toes "two-thirds webbed" or hands "one-half webbed" are convenient for expressing the amount of webbing present, so that quick comparisons can be made between species having noticeably different amounts of webbing. The detailed description of the webbing takes into account the extent of the webbing (exclusive of a dermal fringe on the lateral surface of the phalanx, if present) on each side of each phalanx. Closely related species usually have about the same amount of webbing, but the details of the webbing may differ. For example, the extent of the webbing on the fourth finger is a character by which the Middle American members of the *Hyla boans* group can be distinguished from one another. On the other hand, the vestigial web between the first and second toes is constant in members of the *Hyla rubra* group (fig. 4D). The amount of webbing increases with age and size. The development of the webbing is especially noticeable in large species having nearly fully webbed hands and feet, such as *Agalychnis spurrelli*, *Hyla boans*, *Hyla miliaria*, and *Phrynohyas venulosa*. Consequently, comparisons between adults and juveniles can lead to erroneous conclusions.

COLORATION

Whereas the external structures of hylids are sometimes difficult to describe, the colors and in some species even the patterns are lost in preservative. I have seen living individuals of all but 11 of the species of Middle American hylids. Detailed notes on coloration

tion and hundreds of colored photographs were taken. The importance of these cannot be over-emphasized. The coloration is the easiest way to identify most of the species (see pls. 41-72).

Although the total array of colors in Middle American hylids encompasses the entire visible spectrum, the frogs can be grouped into three categories on the basis of their dorsal ground color (the color that is dominant and exclusive of the markings where present); these are brown, green, and yellow. These basic colors occur in a ratio of 4:3:1, respectively. Thus, brown species outnumber yellow species four to one and are 25 per cent more frequent than green species. The patterns of the frogs can be roughly sorted into three types: plain, striped, and blotched or spotted. The ratio of blotched to plain to striped frogs is 8:6:1. By comparing pattern with dorsal ground color, we find that by far the most common combination is a brown frog with a blotched pattern (46 species), whereas eight brown species are plain and only four are striped. Of the 42 green species, 29 lack a dorsal pattern, and none is striped. Six of the 16 predominantly yellow species are plain, whereas four each are blotched or striped.

The pattern on the dorsal surfaces of the limbs consists of transverse markings of varying widths and distinctness in most species having a blotched or spotted pattern on the back. In most plain species, the dorsal surfaces of the limbs are unmarked or have small darker flecks. Of the eight species that have a dorsal body pattern of stripes, only some populations of three of those species (*Hyla ebraccata*, *microcephala*, and *staufferi*) have linear patterns on the limbs. The thighs are unpigmented, or nearly so, in several small species, for example, members of the *Hyla leucophyllata* and *microcephala* groups. Pigment is lacking in the axilla and groin in some stream-breeding frogs, such as members of the *Hyla bistincta* group and the genus *Plectrohyla*. In many species of green frogs, especially those lacking dorsal markings, the outer edges of the forearms and feet are marked by a pale cream or white stripe, usually in these frogs, such as *Agalychnis* and members of the *Hyla uranochroa* group, a white line is present on the heel and above the anal opening.

Pale labial stripes are common among green frogs and those lacking dorsal markings. In other species, vertical bars are present on the lips; these markings are most common in frogs with a blotched dorsal pattern. In some green frogs, such as *Hyla uranochroa* and *Ptychohyla schmidtorum chamulae*, a white spot is present below the eye. Other facial markings include a dark canthal and supratympanic line in many species and a broad dark brown or black postorbital mark that encompasses the tympanum, such as occurs in *Smilisca* and members of the *Hyla eximia* group.

The ventral coloration is much more uniform. In the majority of species, the venter, with the exception of the vocal sac in breeding males is white, creamy white, or pale yellow. In most of the exceptions, such as some species in the *Hyla bistincta* group and members of the genus *Plectrohyla*, the venter is gray. Uniformly dark gray or brown venters occur in *Anotheca*, *Gastrotheca*, *Hemiphractus*, and in *Hyla chaneque* and *taeniopus*. Dark flecks or reticulations are present on the ventral surfaces of *Hyla rivularis*, *pictipes*, and *tica*, whereas bold black spots are present on an otherwise white venter in *Hyla thorectes* and highland populations of *Hyla lancasteri*. *Phyllomedusa venusta* has an orange belly and brown throat and chest, the latter spotted with white.

The colors on the flanks and anterior and posterior surfaces of the thighs are highly diagnostic in many species. In some species, these surfaces are unicolor and strikingly different from the dorsal coloration. For example, in *Hyla loquax* the dull grayish brown dorsum is in sharp contrast to the bright red anterior and posterior surfaces of the thighs. The flanks and thighs are spotted in many species; for example, bright blue spots are present on those surfaces in *Smilisca cyanostricta* and *sila*. Pale yellow vertical bars are in sharp contrast to the otherwise blue flanks of *Agalychnis callidryas*, and vertical black bars stand out boldly against the golden orange flanks and thighs of *Agalychnis calcarifer*. Bold bars of contrasting colors, such as green and black in *Hyla boulengeri*, orange and black in *Hyla rostrata*, and white or pale yellow and black in *Hyla lancasteri*, are present on the posterior surfaces of the thighs in

some species. The webbing on the hands and feet of most species is not distinctively colored, but in some species, the color of the webbing is markedly in contrast with the dorsal and/or ventral color. In the predominantly brown frogs, *Hyla loquax* and *Hyla pseudopuma infucata*, the webbing is red, as it is in the green *Hyla rufitela*. The webbing is blue in *Agalychnis annae* and orange in *Agalychnis moreletii*, *spurrelli*, and *calcarifer*—all species having a green dorsum.

The coloration of the iris is rather uniform within most species, but great differences exist among some species. Unfortunately, the color of the iris usually is lost or greatly altered soon after preservation. In living frogs, the color of the iris is most easily detected in bright sunlight when the pupil is contracted. In most Middle American hylids, the iris is a golden or bronze color with black flecks or reticulations. Some notable exceptions do exist. Frogs in the *Hyla albomarginata* and *boans* groups have creamy white irises with faint darker reticulations, and members of the *Hyla parviceps* group have an iris that is silvery gray with a red periphery, whereas that in *Phyllomedusa lemur* is uniform silver. A deep copper colored iris occurs in some species, notably *Anothea spinosa* and *Hyla salvadorensis*, and the iris is orange in *Agalychnis annae*. A red iris occurs in nine species. In five species of *Agalychnis* and the two species of the *Hyla uranochroa* group, the iris appears to be covered with red enamel, whereas in *Hyla legleri* and *Hyla erythromma* the iris is a metallic red. I have no knowledge of the histological structure which might help to explain differences in these two kinds of red eyes.

Geographic Variation in Color

Minor differences in color and/or pattern are common in many species of hylids. Usually the amount of variation within samples is nearly as great as that between samples; consequently, meaningful analyses of geographic variation in coloration is not possible for most species. However, notable geographic variation is apparent in a few species. The dorsum is uniform reddish brown in *Ptychohyla schmidtorum* on the Pacific slopes of Guate-

mala and Chiapas and is bright green on the Atlantic slopes of Chiapas. Geographic variation in dorsal pattern occurs in *Hyla eximia*, *microcephala*, and *staufferi* and in *Phrynohyas venulosa*. In the former, the dorsal pattern is highly variable (plain, spots, or linear arrangement of spots), but the percentage of individuals having the different patterns varies geographically. In northern populations of *Hyla microcephala*, the dorsal pattern consists of irregular and interconnected lines and dashes; in southern populations, the pattern consists of parallel longitudinal lines. Northern and southern populations of *Hyla staufferi* differ in the markings on the dorsal surfaces of the shanks. The dorsal pattern in *Phrynohyas venulosa* consists of a large dorsal blotch. In western México, the blotch is fragmented transversely in most specimens, whereas many specimens in eastern México have the blotch longitudinally divided anteriorly. Many specimens from lower Central America have a narrower blotch than do those from the northern part of the range. A unicolor variety of *Phrynohyas venulosa* occurs in Central America and southern México; intermediate coloration exists between the normal pattern of a large blotch and the unicolor variety.

The color of the flanks in *Agalychnis callidryas* varies from dull bluish brown to deep bluish purple, and the presence or absence of a longitudinal white line and the number of vertical white bars varies geographically. *Hyla pseudopuma* has tan webs and posterior surfaces of the thighs throughout most of its range, but on the Atlantic slopes in Panamá, the webs and thighs are red.

Polymorphism

Some species of Middle American hylids exhibit a variation in coloration that seems to be polymorphic. The generally accepted definition of polymorphism is "the simultaneous occurrence of several discontinuous phenotypes or genes in a population, with the frequency of the rarest type higher than can be maintained by recurrent mutation" (Mayr, 1963, p. 670). Goin (1960b and papers cited therein) and Lynch (1966a) have documented cases of pattern polymorphism in *Eleutherodactylus*. Volpe (1955 and 1961) com-

mented on this kind of variation in *Rana*, and Pyburn (1961) discussed the occurrence of polymorphism in *Acris*.

Evidence for pattern polymorphism in Middle American hylids is circumstantial. The small series of *Hyla altipotens* and *pinorum* available each contain individuals having a dorsal pattern of blotches and others with a middorsal stripe. The dorsal patterns are of four types in *Hyla ebraccata*: plain, spotted, triangle, or hour-glass. All specimens can be allocated to one of these four types; intermediate patterns apparently are lacking. Large series of specimens or preferably breeding experiments are desirable in order to determine if these species actually do exhibit pattern polymorphism.

Sexual Dimorphism

The most common kind of sexual color difference is in the development of a pigmented vocal sac in the breeding males of many species. In the small yellow species of *Hyla* in the *microcephala*, *picta*, and *leucophyllata* groups, the vocal sacs are bright yellow in breeding males, whereas in other species, the vocal sacs are either white, dark gray, or brown.

The dorsal coloration usually is not sexually dimorphic, but two notable exceptions occur in Middle American hylids. In males of *Hyla pictipes*, the dorsum is green with dark brown or black mottling; in females, the dorsum usually is uniform green. Furthermore, in females numerous yellow spots are present on the flanks and thighs; these are inconspicuous or absent in males. In the Central American *Hyla subocularis* and the South American members of the *Hyla parviceps* group, the females have a conspicuous dorsolateral pale band, which is absent in males. Females of *Hyla chaneque* and in some populations of *Hyla taeniopus* tend to have darker venters than the males.

Ontogenetic Change

Few of the diagnostic features of the adult coloration are evident in recently metamorphosed young. Bars, spots, or mottling on the flanks and thighs develop after the dorsal and ventral pattern are evident. Even the color of the iris changes with age in some species.

Ontogenetic change in coloration is well documented in few species; these are discussed below.

Juveniles of *Smilisca baudinii* are uniformly dull green above and lack markings on the thighs and flanks. Characteristically, they have a broad white or pale cream spot below the eye; this spot persists as a pale area between dark vertical bars on the lips of adults, which develop large blotches on the dorsum, transverse bars on the limbs, and mottling on the flanks. Juveniles of *Hyla taeniopus* are bright green with numerous black flecks on the dorsum. With increased size, there is a gradual change from many small black flecks to fewer large spots, which in many specimens are fused to form irregular blotches. In *Hyla angustilineata* the young have a bright green dorsum, which changes to brown in adults. Juveniles of *Pternohyla fodiens* are green, usually without a pattern; whereas adults are tan with brown blotches.

A striking ontogenetic change takes place in the coloration of the flanks and thighs in *Smilisca cyanosticta*. Recently metamorphosed young have pale tan flanks, and the posterior surfaces of the thighs are orange-yellow; spots are absent. Slightly larger juveniles have tan flanks and red thighs, both lacking spots; later the flanks become dark brown with blue spots, and the thighs remain the same. Adults have dark brown flanks and thighs, both with blue spots.

The development of color pattern in *Agalychnis callidryas* was described by Starrett (1960a, p. 30), who noted that the white lateral stripe did not develop until about the time the tail was completely absorbed; the blue color and vertical white bars on the flanks did not develop until several weeks later.

In most of those hylids having a golden or bronze-colored iris in adults, the iris in juveniles is pale golden without apparent dark flecks or reticulations. Juveniles of *Hyla taeniopus* have a metallic green iris; larger individuals have a pale bronze iris, and adults have a bronze iris with a darker, copper-colored periphery. The deep red iris of *Hyla rufioculis* and *uranochroa* develops in the tadpoles, but the red iris in *Agalychnis* de-

velops after metamorphosis. Juveniles of *Agalychnis callidryas* have a yellow iris; the red color develops about two weeks after metamorphosis (Starrett, 1960a, p. 30).

Metachrosis

The ability to change color is well documented in hylids (see Duellman, 1961c, Duellman and Trueb, 1966, and Duellman and Fouquette, 1968, for comments on Middle American species). Metachrosis is the rule, rather than the exception, in most of the species. Parker (1948) summarized previous work, mostly experimental in laboratories, on amphibian color changes and stated that frogs respond to cool dark environments by the release of melanophorotropic hormone and darkening of the integument, whereas light and warmth result in melanophore contraction and light colors through the retention or nonsecretion of hormones by the pituitary. Edgren (1954) carried out laboratory experiments on *Hyla versicolor* and concluded that *versicolor* responds to light by the expansion of melanophores and to darkness by the contraction of the melanophores. Thus, according to Edgren, *Hyla versicolor* is paler at night than by day. The contradictory nature of these reports is supported by field observation on Middle American hylids. Most of the species can be grouped into one of two categories depending on the positive or negative correlation of color with the amount of light.

Many pond-breeding species are conspicuously paler at night than by day. Notable examples include the members of the *Hyla godmani*, *leucophyllata*, *microcephala*, and *picta* groups, plus *Hyla elaeochroa* and *staufferi*. In many of these species, the entire dorsum is pallid at night, and the dorsal pattern is faint and inconspicuous. By day, the dorsal ground color is darker and the markings are conspicuous. *Hyla miotympanum* is pale green at night and changes to dark green or mottled green and brown by day (pl. 56).

Contrary to the darker coloration by day characteristic of the groups listed above, other species are darker at night. *Hyla arenicolor* and *crepitans* are brown at night; both are capable of changing to pale tan or pale ashy gray by day. The colors in the various species of *Agalychnis* are darker and more intense at

night. Striking changes take place in *Agalychnis saltator* and *Phyllomedusa lemur*. At night, both species are brownish lavender, and by day they are pale green (pls. 42 and 43).

The two opposing trends in color change do not seem to be correlated with habits or habitat, and at this time no reasonable explanation for differential reaction to light stimulus is available.

TADPOLES

The tadpoles reflect different kinds of adaptations to entirely different environments from the adults. Consequently, correlation between the larval features and those of the adults frequently is lacking. A great variety of morphological types is present among the Middle American hylid frogs. One of our foremost students of tadpoles, Priscilla Starrett, once said that the most bizarre type of tadpoles develop into ordinary frogs, whereas highly distinctive species of frogs usually have very ordinary looking tadpoles. This observation, which might be termed Starrett's Law, certainly seems to hold true for the Middle American hylids. *Hyla zeteki* and *sumichrasti*, as examples, have no very distinctive features as adults, but as tadpoles they are highly modified. On the other hand, the bizarre casque-headed species of *Triprion* have very ordinary tadpoles that are difficult to distinguish from the majority of other pond-type of tadpoles.

All tadpoles have been staged according to Gosner's (1960) developmental table. Accurate comparisons can be made between individuals of the same developmental stage; if differences exist between two tadpoles in different developmental stages, these differences possibly are due to the relative ages of the tadpoles. Whenever possible, I have selected for purposes of description, tadpoles in developmental stages 28 through 34, because after considerable experience, I have found that in these stages the mouthparts are fully developed, and no obvious metamorphic modifications have taken place. Measurements of small tadpoles were made with the aid of an ocular micrometer and a dissecting microscope; the larger tadpoles were measured with dividers under a dissecting microscope. The body length is that distance be-

tween the tip of the snout and the posteroventral edge of the body, and the tail length is taken from the posteroventral edge of the body to the tip of the tail (fig. 12). In relatively unmodified tadpoles the length of the tail is approximately two-thirds of the total length of the tadpole. The relative length of the tail to that of the entire tadpole is given as less than two-thirds ($< 2/3$), equals two-thirds ($= 2/3$), or greater than two-thirds ($> 2/3$). The shape of the body is described as follows: ovoid (depth equal to width), robust (depth slightly greater [$< 15\%$] than width), deep (depth much greater [$\geq 15\%$] than width), or depressed (depth less than width). The relative depths of the caudal fins and of the caudal musculature are based on proportions taken at the midlength of the tail and are given as the relative depth of the dorsal and/or ventral fin to the caudal musculature. The dorsal caudal fin can be described as follows: normal (present throughout length of tail but not extending anteriorly onto the body), or reduced (depth greatly reduced or fin absent on part of tail). Most hylid frogs have a sinistral spiracle and a dextral anal tube (cloaca). The position of the spiracle and the direction of the spiracular opening is of some taxonomic importance.

The position and structure of the mouth is one of the most obvious characters in tadpoles (fig. 13). Among the Middle American hylids, four different positions of the mouth are evident. These are dorsal, terminal, anteroventral, and ventral. In some species, the mouth is situated anteroventrally but directed ventrally; for purposes of analysis, these tadpoles are considered to have a ventral mouth. The width of the mouth is given in relation to

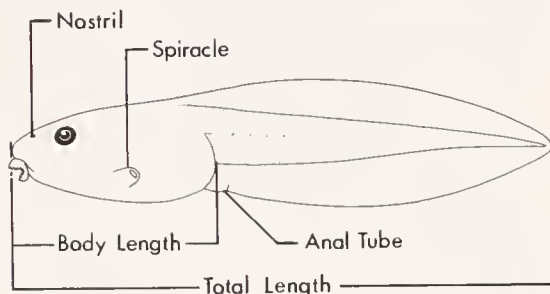


FIG. 12. Hylid tadpole showing certain structures and places of measurements.

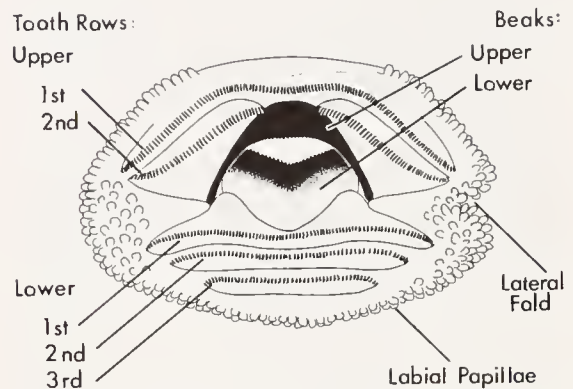


FIG. 13. Diagrammatic view of the mouth of a generalized hylid tadpole showing labial and buccal structures.

the greatest width of the body; although this is an extremely difficult character to measure, I have attempted to categorize the relative size of the mouth. In general terms, I recognize the tadpoles having three sizes of mouths; these are small (less than two-thirds of the width of the body), medium (greater than two-thirds of the width of the body, but less than the width of the body), and large (width of the mouth greater than the width of the body). In most hylid tadpoles, the lips are infolded laterally, but in some species the folds are lacking, and in others the mouth is expanded into a funnel-like structure. The edge of the mouth is either completely or partially bordered by one or more rows of papillae; if the mouth is only partially bordered, at least the median part of the upper lip is devoid of papillae. The number of rows of papillae is a taxonomically important character. Usually only one or two rows of fringing papillae are present; however, in some groups the papillae are much more numerous. For example, in *Hyla rivularis* there are four to six rows of papillae on the lower lip. In tadpoles of the *Hyla bistincta* group and in the genus *Plectrohyla*, the fringing rows of papillae are bordered medially by an irregular row of noticeably larger papillae.

There are many morphological adaptations in tadpoles of Middle American hylids. These adaptations are closely correlated with the environments in which the tadpoles develop. Usually those tadpoles that develop in ponds

have relatively short, high caudal fins and rather slender caudal musculature. These tadpoles have either an anteroventral or an anterior mouth. Tadpoles that develop in streams usually have proportionately much longer tails with lower fins and more robust caudal musculature. Furthermore, these tadpoles have either an anteroventral or ventral mouth which in many species is enlarged and modified into a sucker-like apparatus for at-

tachment to rocks in streams. Tadpoles that develop in bromeliads usually have relatively long tails with heavy caudal musculature and reduced fins (fig. 14).

The size, shape, and structure of the horny beaks are useful taxonomic characters (fig. 15). Well-developed beaks are present in all known Middle American hylid tadpoles; in most of these, the beaks have some kind of serration. The horny "teeth" in tadpoles are arranged on transverse ridges and termed "tooth rows." The majority of hylid frogs have two upper (anterior) rows of teeth and three lower (posterior) rows. Some species lack teeth entirely, whereas other Middle American species have as many as seven upper and 11 lower rows. Although the number of tooth rows is highly important taxonomically, the lateral extent of the rows and the presence of medial interruptions is also significant.

Unfortunately the colors of tadpoles change more drastically than those of the adults once the animals are placed in preservative. Some kinds of tadpoles actually have gaudy coloration; this is especially true of those of the South American groups. For example, the tadpole of *Hyla ebraccata* has broad vertical red, white, and black bands on the tail; in *Hyla microcephala*, the caudal fins are transparent except for an orange periphery. The tadpoles of *Agalychnis* usually are pale blue in life. Although the subtle colors disappear in preservative, some aspects of the pattern usually are evident. The presence of bold mottling or transverse bands on the tail are useful characters in aiding in the identification of certain tadpoles.

Tadpoles of only 84 of the species of Middle American hylid frogs are known. Consequently, a key has not been prepared for the identification of the tadpoles. Instead, a table of the diagnostic features has been prepared (table 2). I think that the diagnostic characters listed therein, in combination with the descriptions given in the text should suffice for the identification of any of the known hylid tadpoles from Middle America.

Several generalities can be drawn from the analysis of the features of the tadpoles of Middle American hylid frogs. For example, the combination of two upper and

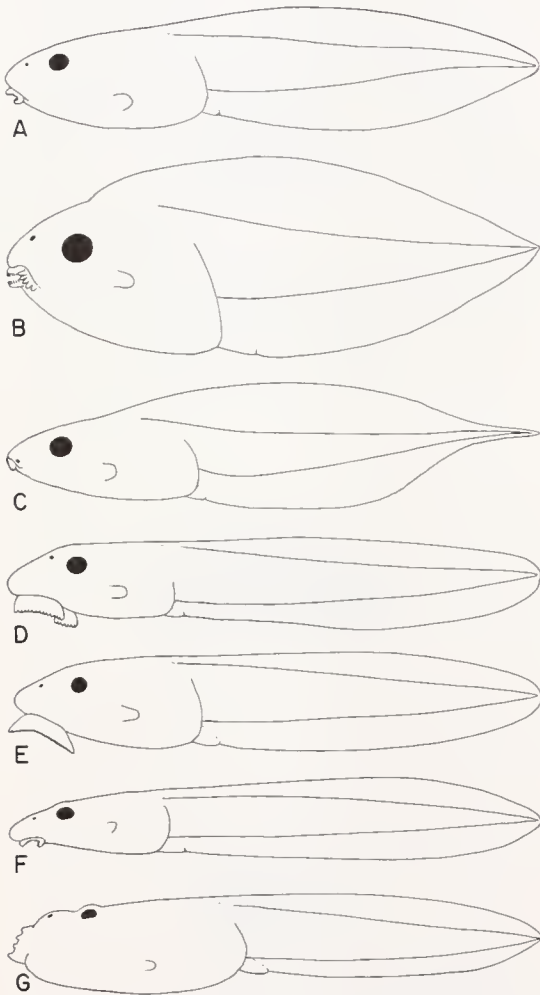


FIG. 14. Body shapes of tadpoles of Middle American hylids. A-C. Pond types: A. *Smilisca puma*. B. *Hyla boulengeri*. C. *Hyla phlebodes* with xiphicercal tail. D and E. Stream types: D. *Hyla rivularis* with enlarged mouth and folded lips. E. *Hyla uranochroa* with funnel-shaped mouth. F and G. Bromeliad types: F. *Hyla bromeliacia* with depressed body. G. *Hyla zeteki* with anterodorsal mouth.

three lower rows of teeth is prevalent in tadpoles from various geographic regions and inhabiting various ecological situations. However, the presence of more than two upper and three lower rows of teeth in pond-type tadpoles occurs only in South American groups [*Hyla albomarginata* and *boans* groups (2/4) and *Phrynohyas* (3/4-6)]. The number of rows of teeth is reduced in egg-eating tadpoles (1/1 in *Hyla zeteki*; 2/2 in *Anotheca*). However, *Acris crepitans* also has only two upper and two lower rows of teeth. Rows of teeth are absent only in those tadpoles having terminal mouths, and these belong only to certain South American groups (*Hyla leucophyllata*, *microcephala*, and *parviceps* groups). In these same groups, the tails are xiphicercal; a tendency toward this type of tail also is present in some members of the South American *Hyla rubra* group.

The greatest proliferation of tooth rows is found in tadpoles inhabiting streams. Here it is interesting to note that although there are numerous stream adapted tadpoles in the highlands of lower Central America and that many of these tadpoles have enlarged mouths (such as *Hyla pictipes* and *rivularis*), the great majority of species do not have a proliferation of tooth rows. On the other hand, the enlargement of the mouth in tadpoles in the highlands of Central America and in the highlands of México usually is accompanied by a proliferation of tooth rows. Two exceptions are noted in lower Central America; these are *Hyla legleri* (an apparent invader from the north) having two upper and five lower rows of teeth, and *Hyla colymba* (apparently a South American species) having six upper and nine lower rows of teeth. Not all of the stream tadpoles in northern Middle America have enlarged mouths and an increased number of tooth rows. For example, the stream-adapted tadpoles of the *Hyla bistincta* group and of *Plectrohyla* all have two upper and three lower rows of teeth contained in a relatively small mouth. However,

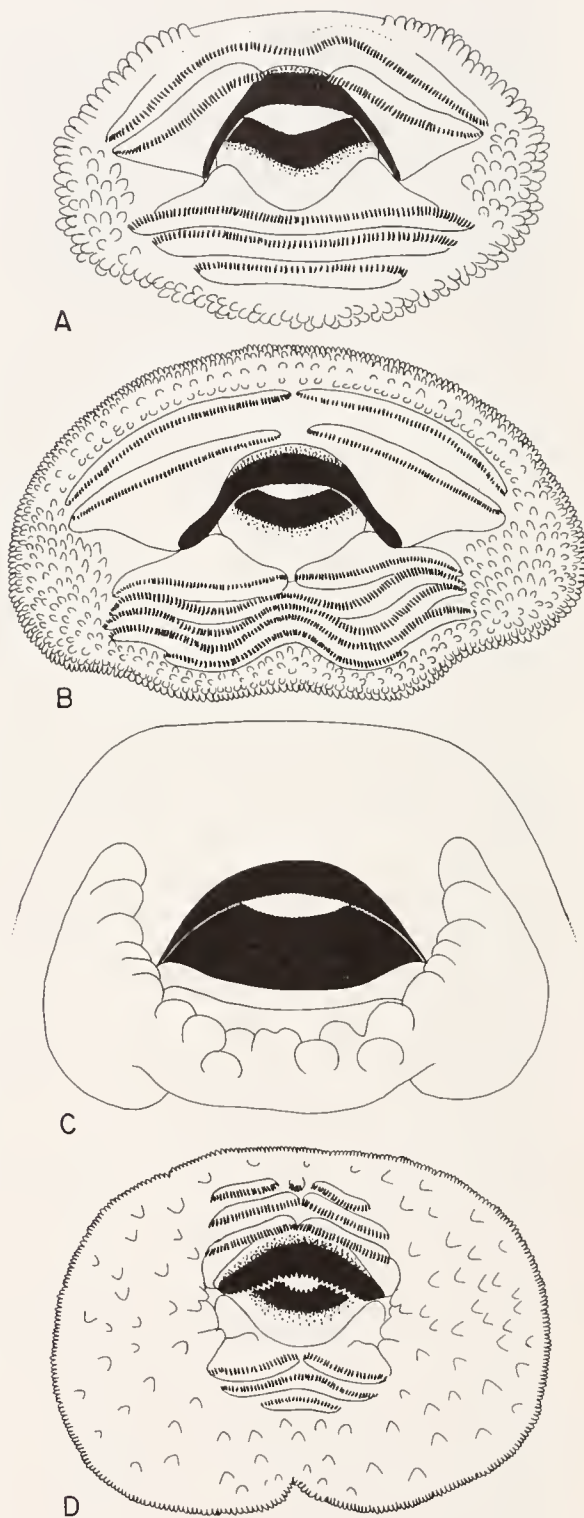


FIG. 15. Mouths of hyloid tadpoles showing adaptive modifications. A. Generalized pond type, *Smilisca puma*. B. Enlarged and ventral stream type, *Hyla pinorum*. C. Terminal pond type, *Hyla ebraccata*. D. Funnel-shaped stream type, *Ptychohyla ignicolor*.

these tadpoles do have moderately long, tremendously muscular tails with low fins and a ventral mouth. One of the most striking modifications of the mouth in Middle American hylid tadpoles is the development of a funnel-shaped mouth. This type of mouth is present in two closely related species of the *Hyla uranochroa* group in lower Central America and in two closely related species of *Ptychohyla* in México and Guatemala. In these tadpoles the mouth has a complete border that is expanded and bears few small papillae on the border. It is interesting to note that tadpoles having mouths such as these have not only a reduced number of tooth rows, but the length of the existing rows is greatly reduced. It seems as though the teeth in these tadpoles are less important in grasping or holding than in those tadpoles not having a funnel-shaped mouth.

The careful study of the larval morphology and a comparison of the physical features of the tadpoles with the environment in which they live provide certain clues towards general evolutionary trends in hylid tadpoles. It seems only reasonable that the generalized type of pond-tadpole probably most closely approximates the larva of the hylid prototype. I visualize a primitive hylid tadpole to be a pond dweller and to have an ovoid body, tail equal to about two-thirds of the total length, moderately developed caudal musculature, generalized caudal fins probably not extending onto the body and equal in depth to the caudal musculature, a medium or small anteroventral mouth having an incomplete fringe of labial papillae, moderate lateral folds and two upper and three lower rows of teeth. A tadpole of this type approximates the generalized leptodactylid tadpoles and therefore is in line with the present concepts of the ancestry of the family *Hylidae*.

From a generalized hylid tadpole three general evolutionary trends are evident, into the streams (lotic), ponds (lentic), and arboreal environments. Adaptations for the lotic environments include shallower, more streamlined body, a proportionately longer tail with heavier caudal musculature and shallower fins, and a large ventral mouth. The modifications of the mouth are divergent at this point into either a greatly enlarged mouth with an

increased number of tooth rows and a proliferation of labial papillae or to a funnel-shaped with the loss of the lateral fold and a reduction in the number of teeth and papillae. The adaptations to a lentic environment include an increased depth of the fins, the extension of the dorsal fin onto the body, which is deep. Further modifications include the development of a ventral spiracle, or the development of a terminal mouth lacking teeth and papillae. Arboreal adaptations include the development of a long tail with reduced fins and a ventral mouth, or a mouth modified for eating frog eggs.

One thing is obvious from the examination of the tadpoles and the correlation of the larval characteristics with the features of the adults; the various structural modification of the tadpoles do not necessarily indicate phylogenetic relationships. In other words, all species of hylid frogs having tadpoles adapted for a stream existence are not necessarily related to one another. Likewise, frogs having arboreal tadpoles are not necessarily related. By taking a generalized pond-type tadpole as an example of a primitive hylid, I have implied the evolutionary direction from pond to stream and from pond to arboreal habitat for hylid tadpoles. Likewise, I have indicated the evolutionary direction of various physical modifications of the tadpoles. The evolutionary trends in the mouthparts of stream tadpoles is for an increase in the size of the mouth, the development of a complete labial fringe of papillae, an increase in the number of rows of papillae, and an increase in the number of rows of teeth. Consequently, it is entirely possible that in México, the rather generalized stream tadpole of *Hyla miotympanum* could have developed from a generalized pond-type of tadpole and could have given rise to the tadpole of *Hyla arboreascendens*, which differs from *miotympanum* by having one additional lower row of teeth and by having the labial border completely bordered by papillae. A tadpole of the *Hyla arboreascendens*-type could have given rise to tadpoles of the *Hyla pinorum* group by the addition of one more lower row of teeth and one more row of fringing papillae. The addition of one more upper row and one more lower row of teeth would result in the tad-

TABLE 2
Diagnostic Features of the Known Tadpoles of Middle American Hyliids.

Species (Arranged by Tooth Row Formula)	Mouth	Number and Position of Rows of Labial Papillae	Serrations on Beaks	Shape of Body	Tail- Body Ratio	Depth of Dorsal Fin to Musculature; Modification of Fins
Tooth Rows 0/0						
<i>Hyla ebraccata</i> ^{a,b}	Term.; small	One; lower	Fine	Ovoid	> 2/3	>; on body
<i>Hyla parviceps</i> ^{a,b}	Term.; small	One; lower	Fine	Ovoid	= 2/3	>; normal
<i>Hyla microcephala</i> ^{a,b}	Term.; small	None	Fine	Ovoid	< 2/3	>; on body
<i>Hyla phlebodes</i> ^{a,b}	Term.; small	None	Fine	Ovoid	= 2/3	>; on body
Tooth Rows 1/1						
<i>Hyla zeteki</i> ^b	Dorsal; med.	One; complete	Upper smooth; lower fine	Depressed	> 2/3	<; reduced
Tooth Rows 2/2						
<i>Acris crepitans</i>	Antven.; small	One; incomplete	Fine	Deep	< 2/3	>; on body
<i>Anotheca spinosa</i>	Antven.; small	One; complete	Fine	Depressed	< 2/3	<; normal
<i>Hyla rufoculis</i> ^{b,c}	Ventral; large; funnel-shaped	One; complete	Long; pointed	Ovoid	> 2/3	<; normal
<i>Hyla uranochirod</i> ^{b,c}	Ventral; large; funnel-shaped	One; complete	Long; pointed	Ovoid	> 2/3	<; normal
Tooth Rows 2/3						
<i>Pseudacris clarkii</i>	Antvent.; small	1 or 2; incomplete	Short; conical	Deep	< 2/3	>; on body
<i>Hyla arenicolor</i>	Antvent.; small	1 or 2; incomplete	Fine	Ovoid	< 2/3	=; on body
<i>Hyla cadaverina</i>	Ventral; med.	Two; incomplete	Fine	Elliptical	< 2/3	=; on body
<i>Hyla regilla</i>	Antvent.; small	Two; incomplete	Fine	Deep	< 2/3	=; on body
<i>Hyla eximia</i>	Antvent.; small	Two; incomplete	Fine	Deep	< 2/3	>; on body
<i>Hyla euphorbiacea</i>	Antvent.; small	Two; incomplete	Fine	Deep	< 2/3	>; on body
<i>Hyla walkeri</i>	Antvent.; small	Two; incomplete	Fine	Deep	< 2/3	>; on body
<i>Hyla miotympanum</i>	Ventral; med.	One; incomplete	Blunt	Ovoid	= 2/3	=; normal
<i>Hyla thorectes</i>	Ventral; small	One; complete	Large; pointed	Ovoid	= 2/3	<; normal
<i>Hyla altipotens</i>	Ventral; small	2 or 3; complete	Long; blunt	Ovoid	< 2/3	<; on body

TABLE 2—(Continued)

Species (Arranged by Tooth Row Formula)	Mouth	Number and Position of Rows of Labial Papillae	Serrations on Beaks	Shape of Body	Tail- Body Ratio	Depth of Dorsal Fin to Musculature; Modification of Fins
<i>Hyla taeniopus</i>	Antvent.; small	2 or 3; complete	Fine	Ovoid	<2/3	>; normal
<i>Hyla bistincta</i> ^d	Ventral; med.	Two; complete	Peg-like	Depressed	>2/3	=; on body
<i>Hyla pentheter</i> ^d	Ventral; med.	1 or 2; complete	Large; blunt	Depressed	=2/3	<; on body
<i>Hyla robertsoni</i> ^d	Ventral; med.	Two; complete	Peg-like	Depressed	=2/3	<; on body
<i>Hyla bogertae</i> ^d	Ventral; med.	Two; complete	Fine	Depressed	=2/3	=; normal
<i>Hyla siopela</i> ^d	Ventral; small	Two; complete	Pointed	Depressed	<2/3	>; normal
<i>Hyla picta</i>	Antven.; small	One; incomplete	Fine	Deep	=2/3	>; on body
<i>Hyla godmani</i>	Antven.; small	2 or 3 incomplete	Short; conical	Ovoid	<2/3	>; on body
<i>Hyla loquax</i>	Antven.; small	One; incomplete	Pointed	Ovoid	<2/3	>; on body
<i>Hyla pseudopuma</i>	Ventral; small	Two; incomplete	Small; pointed	Robust	<2/3	=; normal
<i>Hyla angustilineata</i>	Ventral; small	Two; incomplete	Short; pointed	Robust	<2/3	<; normal
<i>Hyla lancasteri</i>	Ventral; small	Two; complete	pointed	Depressed	=2/3	<; normal
<i>Hyla debilis</i>	Ventral; large	2 or 3; complete	Long; fine	Depressed	>2/3	=; normal
<i>Hyla rivularis</i>	Ventral; huge	Three; complete	Fine	Depressed	>2/3	=; on body
<i>Hyla tica</i>	Ventral; large	Two above; 4-6 below	Minute	Depressed	>2/3	>; normal
<i>Hyla pictipes</i>	Ventral; huge	Two above; 4-6 below	Minute	Depressed	<2/3	<; normal
<i>Hyla rubra</i> ^a	Antven.; small	1-3; incomplete	Fine	Deep	=2/3	>; on body
<i>Hyla elaeochroa</i>	Antven.; small	1-3; incomplete	Fine	Deep	=2/3	>; on body
<i>Hyla staufferi</i>	Antven.; small	1 or 2; incomplete	Fine	Deep	<2/3	>; on body
<i>Hyla rostrata</i> ^a	Antven.; small	One; incomplete	Long; pointed	Deep	>2/3	>; on body
<i>Hyla boulengeri</i>	Antven.; small	One laterally	Long; pointed	Deep	=2/3	>; on body
<i>Plectrohyla matudai</i> ^d	Ventral; med.	One; complete	Long; pair enlarged	Ovoid	=2/3	<; normal
<i>Plectrohyla ixil</i> ^a	Ventral; med.	One; complete	Long; unequal	Ovoid	=2/3	<; normal
<i>Plectrohyla sagorum</i> ^d	Ventral; med.	One; complete	Long; equal	Ovoid	<2/3	<; normal

TABLE 2—(Continued)

Species (Arranged by Tooth Row Formula)	Mouth	Number and Position of Rows of Labial Papillae	Serrations on Beaks	Shape of Body	Tail- Body Ratio	Depth of Dorsal Fin to Musculature; Modification of Fins
<i>Plectrohyla quechchi</i> ^d	Ventral; med.	One; complete	Long; equal	Ovoid	<2/3	<; normal
<i>Plectrohyla glandulosa</i> ^d	Ventral; med.	One; complete	Short; pointed	Ovoid	<2/3	<; normal
<i>Plectrohyla guatemalensis</i> ^d	Ventral; large	Two; complete	Short; blunt	Ovoid	<2/3	<; normal
<i>Smilisca baudinii</i>	Antven.; small	Two; incomplete	Blunt	Robust	<2/3	>; on body
<i>Smilisca cyanosticta</i>	Antven.; small	One; incomplete	Fine	Robust	<2/3	>; normal
<i>Smilisca phaeota</i>	Antven.; small	One; incomplete	Blunt	Robust	<2/3	>; on body
<i>Smilisca puma</i>	Antven.; small	One; incomplete	Fine	Ovoid	<2/3	>; on body
<i>Smilisca sila</i>	Ventral; med.	1 or 2	Blunt	Ovoid	=2/3	=; normal
<i>Smilisca sordida</i>	Ventral; large	incomplete				
<i>Pternohyla fodiens</i>	Antven.; small	Two; complete	Blunt	Ovoid	>2/3	=; normal
		1 or 2	Small; pointed	Ovoid	<2/3	>; normal
<i>Tripion petasatus</i>	Antven.; small	incomplete				
<i>Pachymedusa dacnicolor</i> ^e	Antven.; small	One; incomplete	Small; pointed	Ovoid	<2/3	>; on body
<i>Agalychnis saltator</i> ^e	Antven.; small	One; incomplete	Small; pointed	Deep	<2/3	=; normal
		1 or 2;	Short; pointed	Robust	=2/3	=; normal
<i>Agalychnis callidryas</i> ^e	Antven.; small	incomplete				
		1-3;	Blunt	Robust	<2/3	=; normal
<i>Agalychnis moreletii</i> ^e	Antven.; small	incomplete				
<i>Agalychnis annae</i> ^e	Antven.; small	Two; incomplete	Short; pointed	Deep	<2/3	=; normal
<i>Agalychnis spurrelli</i> ^e	Antven.; small	Two; incomplete	Short; pointed	Deep	=2/3	=; normal
		2 or 3;	Short; pointed	Robust	<2/3	=; normal
<i>Phyllomedusa lemur</i> ^e	Antven.; small	incomplete				
		2 or 3;	Fine	Robust	<2/3	=; on body
		incomplete				
Tooth Rows 2/4						
<i>Hyla arboreascendens</i>	Ventral; med.	One; complete	Long; pointed	Ovoid	>2/3	=; normal
<i>Hyla chaneque</i>	Antven.; med.	2 or 3;	Long; pointed	Ovoid	<2/3	<; normal
		complete				
<i>Hyla dendroscarta</i>	Ventral; small	Two; incomplete	Short; pointed	Depressed	>2/3	<; reduced
<i>Hyla bromeliacia</i> ^{b, f}	Ventral; small	Two below	Long; pointed	Depressed	>2/3	<; reduced

TABLE 2—(Continued)

Species (Arranged by Tooth Row Formula)	Mouth	Number and Position of Rows of Labial Papillae	Serrations on Beaks	Shape of Body	Tail- Body Ratio	Depth of Dorsal Fin to Musculature; Modification of Fins
<i>Hyla crepitans</i>	Antven.; small	One; incomplete	Fine	Robust	$\approx 2/3$	>; normal
<i>Hyla rosenbergi</i>	Antven.; small	1 or 2; complete	Fine	Robust	$\approx 2/3$	>; normal
<i>Hyla boans</i>	Antven.; small	One; incomplete	Short; pointed	Robust	$> 2/3$	>; normal
<i>Hyla rufitela</i>	Ventral; small	One; incomplete	Short; pointed	Robust	$< 2/3$	\approx ; normal
Tooth Rows 2/5						
<i>Hyla melanomma</i>	Ventral; med.	One; complete	Long; blunt	Ovoid	$< 2/3$	\approx ; normal
<i>Hyla pinorum</i>	Ventral; med.	Two; complete	Short; blunt	Ovoid	$< 2/3$	<; normal
<i>Hyla legleri</i> ^g	Ventral; large	Two; complete	Short; blunt	Ovoid	$\approx 2/3$	<; normal
<i>Hyla salvadorensis</i> ^g	Ventral; large	Two; complete	Short; blunt	Ovoid	$\approx 2/3$	<; normal
Tooth Rows 3/3						
<i>Ptychohyla schmidtorum</i> ^b ..	Ventral; large; funnel-shaped	One; complete	Long; pointed	Ovoid	$> 2/3$	>; on body
<i>Ptychohyla ignicolor</i> ^b	Ventral; large; funnel-shaped	One; complete	Long; pointed	Ovoid	$> 2/3$	>; on body
Tooth Rows 3/4-6						
<i>Phrynohyas venulosa</i>	Antven.; small	2 or 3; incomplete	Fine	Robust	$< 2/3$	>; on body
Tooth Rows 3/6-7						
<i>Hyla sumichrasti</i> ^d	Ventral; huge	Two; complete	Minute	Depressed	$> 2/3$	\approx ; normal
<i>Hyla smaragdina</i> ^d	Ventral; huge	Two; complete	Small; pointed	Depressed	$< 2/3$	<; normal
Tooth Rows 4/6						
<i>Hyla erythromma</i>	Ventral; large	2 or 3; complete	Blunt	Ovoid	$> 2/3$	<; normal
<i>Ptychohyla euthysanota</i>	Ventral; large	Two; complete	Peg-like	Ovoid	$\approx 2/3$	>; on body
<i>Ptychohyla leonhard-</i> <i>schultzei</i>	Ventral; large	Two; complete	Peg-like	Ovoid	$> 2/3$	>; on body
<i>Ptychohyla spinipollex</i>	Ventral; large	Two; complete	Pig-like	Ovoid	$< 2/3$	>; on body

TABLE 2—(Concluded)

Species (Arranged by Tooth Row Formula)	Mouth	Number and Position of Rows of Labial Papillae	Serrations on Beaks	Shape of Body	Tail- Body Ratio	Depth of Dorsal Fin to Musculature; Modification of Fins
Tooth Rows 6/9						
<i>Hyla colymba</i>	Ventral; large	Two; complete	Long; blunt	Ovoid	<2/3	<; normal
Tooth Rows 7/10 or 11						
<i>Hyla mixomaculata</i>	Ventral; large	One; complete	Smooth	Depressed	=2/3	<; normal
<i>Hyla mixe</i>	Ventral; large	One; complete	Smooth	Depressed	=2/3	<; normal

^a Tail xiphicercal.^b Lips lacking lateral folds.^c Eyes red; a short third lower tooth row present in some specimens.^d Irregular row(s) of large papillae median to row(s) of fringing papillae.^e Spiracle ventral, sinistral to midline.^f Five lower rows of teeth in some individuals.^g Three upper rows of teeth in some individuals.

pole like that found in the *Hyla sumichrasti* group, whereas the addition of a fourth upper row results in the tadpole like that found in the *Hyla erythromma* group, and additional proliferation of tooth rows into seven upper and ten or eleven lower rows results in the highly modified tadpoles characteristic of the *Hyla mixomaculata* group.

Similar types of tadpoles in the highlands of lower Central America and also in the highlands of South America suggest that the morphological modifications of tadpoles for lotic environments have undergone a considerable amount of parallel evolution. Although some of the structures in tadpoles are similar from widely different areas, usually the combinations of structures are sufficiently different, so that the tadpoles can be adequately placed in their own phyletic groups in particular geographic regions.

Whereas the trend in lotic environments is towards the proliferation of mouthparts and elongation of the tail with a corresponding decrease in surface area, the opposite is true in modifications for a truly lentic environment. In the quiet water, the tadpoles maintain their positions by a fluttering action of the posterior part of the tail. In some kinds of tadpoles, such as those in the *Hyla leucophyllata*, *microcephala*, and *parviceps* groups, the tip of the tail is drawn out into a xiphicercal pattern. When in a resting position, only this protruding tip of the tail flutters. The deep caudal fins and the anterior extension of the dorsal fin onto the body aid in providing a tremendously large surface area to the tail, which is powered by relatively weak musculature. The mouth in lotic tadpoles is utilized for maintenance of position by adherence to a rock on the bottom of a stream, whereas the mouth in lentic tadpoles functions only for ingestion of food. Some of the lentic tadpoles feed on aquatic plants; others apparently feed at least partially on phytoplankton. In some of the lentic tadpoles, the labial papillae are reduced in number or completely lost and the teeth are missing, so that the mouth consists merely of a pair of fleshy folds surrounding the horny beaks.

The tadpoles that develop in arboreal situations have certain obvious morphological modifications, principally a small depressed

body and an elongate tail having reduced fins. However, the physiological adaptations must be even more striking than the morphological ones, because these tadpoles develop in extremely limited quantities of water, in which there is a considerable amount of decaying vegetable matter and consequently a relatively low amount of dissolved oxygen. The apparent shortage of food in the arboreal situations (bromeliads or water-filled cavities in trees) has been met successfully by the habit of ingestion of frog eggs. At this time it can only be supposed that the eggs ingested are those of the same species.

A discussion of the tadpoles of Middle American hylids would not be complete without mentioning those species that lack an aquatic larval stage—the two species of *Gastrotheca* and the one of *Hemiphractus* that occur in Middle America. Insofar as known, the eggs of *Gastrotheca* develop directly into small frogs in the brood pouch of the female, whereas the eggs carried on the back of the female *Hemiphractus* develop directly into small frogs, which are attached to the back of the female by four tiny cords (pl. 7).

It is obvious that the evolutionary adaptations of the larval stages of hylid frogs have been extremely important in the dispersal and probably speciation of the group as a whole. Ecological preferences of tadpoles are evident. In some streams, the species of tadpoles segregate nicely into pools versus ripples. In ponds, tadpoles of certain species seek sunny areas, whereas others are found only in the shade. Observations on the ecology and behavior of tadpoles are extremely limited, and much further work remains to be done on this subject. The present observations only hint at the possibilities for future work and understanding.

CRANIAL OSTEOLOGY

Until recently, knowledge of the variation in cranial elements of hylid frogs was extremely meager. Duellman (1964b) used cranial characters in defining the *Hyla bistincta* group. Brief descriptions of cranial structure have been given for *Phrynohyas* (Duellman, 1956a) and *Ptychohyala* (Duellman, 1963c), and specific and sexual differ-

ences in the skulls of *Hyla chaneque* and *taeniopus* were pointed out by Duellman (1965b). Duellman and Trueb (1966), Duellman and Fouquette (1968), and León (1969) used cranial characters in defining species groups and in showing differences between species in *Smilisca* and in the *Hyla microcephala* and *rubra* groups, respectively. Trueb (1968b) presented a description of the internal cranial osteology of *Smilisca baudinii*. The only extensive comparisons of cranial osteology of hylid frogs are in Trueb's (1970a) study of the casque-headed hylids.

Data on the cranial osteology have been accumulated on 101 of the species of Middle American hylids. These data have been especially helpful in defining most of the genera and species groups, although cranial characters are of limited use in some of the groups of stream-breeding hylids in México, in which the cranial elements are considerably reduced. Obvious differences exist in the presence or absence of certain elements or processes, whereas more subtle differences exist in the shapes and relative development of other elements. Most differences occur in the dermal elements.

Several problems have been encountered in the comparative study of the cranial osteology. Generally, the larger individuals of a species have more fully ossified skulls than do smaller individuals, even though the latter are sexually mature. Thus, whenever possible, osteological characters were studied on the largest available specimens. Comparisons between dried and cleared and stained specimens are difficult due to the differential pres-

ervation and to light refraction in cleared and stained specimens; however, an experienced eye can determine the nature of the bones.

Each of the cranial elements and their various processes are defined and the variation in these elements is discussed below. The terminology is the same as used by Trueb (1970a), and the cranial bones are illustrated in figure 16.

Dermal Elements

Angulosphenial: Paired bones in lower jaw lying medial and ventral to Meckel's cartilage. No variation of taxonomic significance was noted.

Dentary: A bone in the lower jaw; it is located anterolaterally to Meckel's cartilage and articulates anteriorly with the mentomeckelian. No variation of taxonomic significance was noted, except the presence of a pair of odontoids anteriorly in *Hemiphractus*.

Dermal Sphenethmoid: The dorsal, dermal component of the endochondral sphenethmoid (fig. 17D). This element, which was first defined by Trueb (1966, p. 563), is co-ossified with the overlying skin, completely fused with the underlying endochondral sphenethmoid, and usually articulated with the nasals anteriorly and frontoparietals posteriorly. This element is present in only two Middle American species, *Gastrotheca ceratophrys* and *Triprion petasatus*.

Frontoparietal: Paired dermal roofing bones overlying the sphenethmoid and prootic. In most hylids, the frontoparietals are separated medially exposing all or part of the frontoparietal fontanelle (fig. 17C).

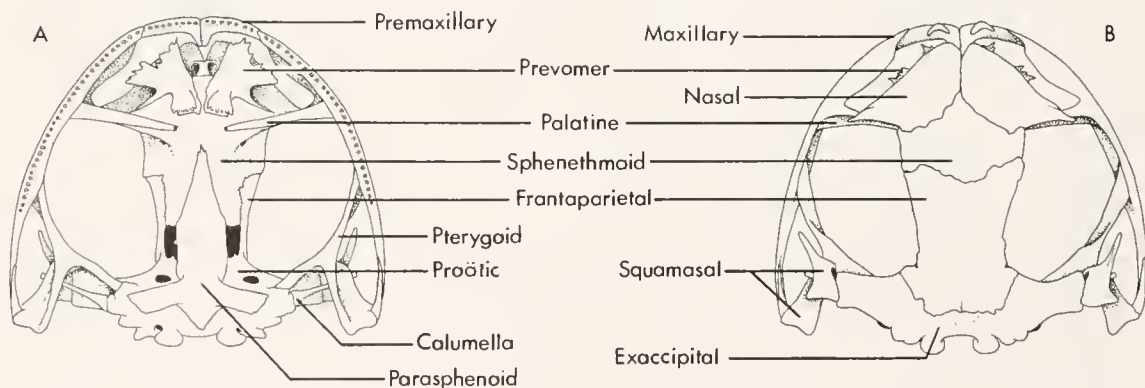


FIG. 16. Ventral (A) and Dorsal (B) views of a generalized hylid skull with terminology of cranial bones.

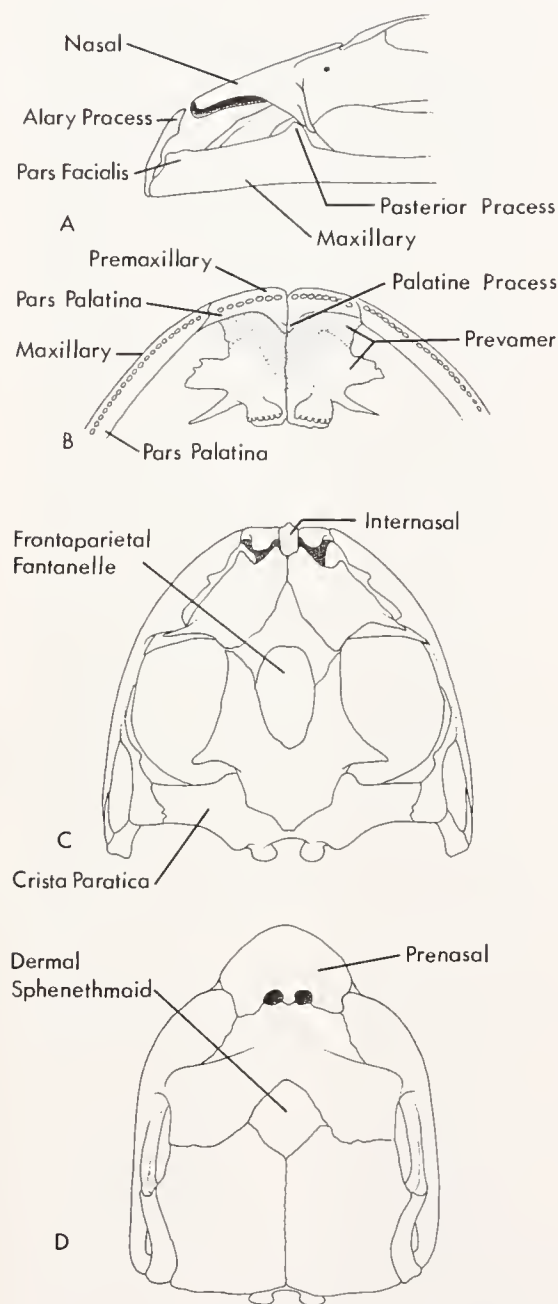


FIG. 17. Cranial characters of hylid frogs. A. Lateral view of anterior part of skull. B. Ventral view of anterior part of skull; shaded area shows extent of prevomers in those species in which they articulate with the premaxillaries. C. Dorsal view showing position of internasal in *Pternohyla fodiens* and nature of frontoparietal flanges in *Smilisca baudinii*. D. Dorsal view of *Triprion petasatus* showing prenasal and dermal sphenethmoid.

This fontanelle is an oval opening in the endochondral cranial roof; the fontanelle is formed in the sphenethmoid anteriorly and the prootic posteriorly and covered by membranous connective tissue. In some species, there is a median encroachment of the frontoparietals over the fontanelle so that the fontanelle appears to be long and narrow; in those species, in which the frontoparietals are not expanded medially, small amounts of calcification occur in the membranous connective tissue covering the fontanelle. The fontanelle is completely covered by the frontoparietals in *Phrynohyas*, *Anotheca*, *Gastrotheca*, *Pternohyla*, *Triprion*, a few species of *Hyla* (especially noteworthy are some members of the *Hyla rubra* group) and one species of *Smilisca* (*phaeota*). The lateral margins of the frontoparietals are straight and even (the normal condition, see fig. 17B) in most species but they are expanded laterally over the orbits in *Anotheca*, *Gastrotheca*, *Phyllomedusa venusta*, *Pternohyla* and *Triprion* and partly so in *Smilisca baudinii* and *phaeota* (fig. 17C).

Internasal: A median roofing bone lying anterior to the nasals and between the external nares (fig. 17C). Trueb (1970a) named this bone and noted its presence in *Pternohyla fodiens*.

Maxillary: Paired dermal dentigerous bones forming the major part of the upper jaw. In all Middle American hylids, teeth are present on the maxillary, which articulates with the premaxillary anteriorly and in some species with the quadratojugal posteriorly. The pars facialis is the dorsomedially inclined flange of bone arising from the dorsal surface of the longitudinal axis of the maxillary (fig. 17A). The pars facialis is absent in *Hyla smaragdina*. In most species, the pars facialis does not articulate with the nasal; partial articulation is present in *Hemiphractus panamensis*, *Hyla picadoi* and *siopela*, *Pternohyla dentata*, *Smilisca puma*, and in members of the *Ptychohyla euthysanota* group. The pars facialis completely articulates with the nasal in *Anotheca*, *Pternohyla fodiens*, and both species of *Triprion*. The posterior process of the pars facialis (fig. 17A) is a dorsal expansion on the posterodorsal surface of the pars facialis. The process is absent in most small

species, in most of the stream-breeding species of *Hyla*, and in the easque-headed frogs of the genera *Pternohyla* and *Triprion*. In the larger frogs (*Anotheca*, *Gastrotheca*, *Hemiphractus*, *Pachymedusa*, *Phrynohyas*, *Phyllomedusa venusta*, *Plectrohyla*, *Smilisca*, and members of the *Hyla albomarginata*, *boans*, *miliaria*, and *taeniopus* groups) plus several medium-sized species of *Hyla*, such as the *Hyla lancasteri*, *pseudopuma*, and *zeteki* groups, and the *euthysanota* group of *Ptychohyla*, the posterior process of the pars facialis articulates with the maxillary process of the nasal. In the other species, the posterior process is present but not articulating with the maxillary process of the nasal. The lingual flange of the maxillary is called the pars palatina (fig. 17B). This flange is conspicuous in *Agalychnis*, *Pachymedusa*, *Phyllomedusa*, *Pternohyla fodiens*, the *euthysanota* group of *Ptychohyla*, *Smilisca* (except *puma*), *Triprion spatulatus*, and several species of *Hyla*. The pars palatina is absent in *Hemiphractus panamensis* and present, but inconspicuous, in other Middle American hylids. A distinct labial flange is present on the maxillary in *Pternohyla* and *Triprion*.

Nasal: Paired dermal roofing bones overlying the olfactory capsules anterior to the sphenethmoid. The nasals are highly variable in shape and in the amount of articulation with other bones. In some species, the nasals are small, slender elements that do not articulate with the sphenethmoid posteriorly or with one another medially. This is the condition characteristic of several species of small *Hyla*, such as *bromeliacia*, *dendroscarta*, *miotympanum*, *phlebodes*, and *pinorum*, plus the large frogs of the *Hyla boans* groups. In most frogs in which the nasals are reduced, the maxillary process of the nasal is absent or not articulating with the posterior process of the pars facialis of the maxillary; frogs of the *Hyla boans* group are an exception. The nasals are expanded and in contact medially with one another and articulate posteriorly with the sphenethmoid in *Anotheca*, *Gastrotheca*, *Hemiphractus*, *Pachymedusa*, *Phyllomedusa*, *Phrynohyas*, *Pseudacris*, *Pternohyla*, *Triprion*, and in members of the *Hyla leucophyllata* and *rubra* groups, plus a scattering of other species of *Hyla*. In *Acris*, *Agalychnis*,

Plectrohyla, *Ptychohyla*, *Smilisca*, and the other species of *Hyla* the nasals are moderately developed.

Palatine: Paired supportive bones at the anterior end of the orbit. In most species, the palatine articulates laterally with the maxillary and medially with the sphenethmoid, whereas the bone is reduced in some species. The palatine lacks an articulation with the sphenethmoid in *Hyla pentheter* and *Triprion petasatus* and an articulation with the maxillary in *Hyla angustilineata* and *walkeri*. The bone is reduced to a small completely non-articulating element in *Hyla sumichrasti* and *Pseudacris clarkii* and absent in *Hyla smaragdina* and *staufferi*. In most species of *Hyla*, all Middle American species of *Acris*, *Agalychnis*, *Gastrotheca*, *Pachymedusa*, *Pseudacris*, and *Ptychohyla*, some species of the genera *Plectrohyla*, *Phyllomedusa*, and *Smilisca*, and in *Triprion petasatus* the ventral surface of the palatine is smooth or bears a smooth ridge. In all other species, an irregular or serrate ridge is present. The ridge is irregular in *Phrynohyas venulosa*, *Phyllomedusa venusta*, *Plectrohyla ixil* and *matudai*, *Pternohyla dentata* and *fodiens*, *Smilisca cyanosticta*, and four species of *Hyla* (*lancasteri*, *miliaria*, *picadoi*, and *tica*), whereas the ridge is noticeably serrate in *Hyla cadaverina*, *Hemiphractus panamensis*, and *Triprion spatulatus*.

Parasphenoid: A median vesting bone ventral to the prootic and the posterior part of the sphenethmoid. Among the Middle American hylids, the parasphenoid is smooth in all species, except the two species of *Triprion*, in which a median longitudinal patch of odontoids is present.

Premaxillary: Paired dentigerous bones forming the anterior margin of the upper jaw and articulating laterally with the maxillaries and medially with one another. The dorsal process of the premaxillary is the alary process (fig. 17A). The alary process is single in all Middle American hylids, except *Plectrohyla*, in which it is bifurcate (fig. 18). The anterodorsal tip of the alary process lies adjacent to the nasal cartilages anteroventral to the nasals, and the posteroventral ramus extends beneath the anterior part of the sphenethmoid, thereby providing support for the en-

tire nasal region and anterior end of the sphenethmoid. The alary processes of the premaxillaries are inclined posteriorly in most species having rounded, or sloping snouts and are vertical in most of those with truncate snouts. The processes are slightly inclined anteriorly in two of the species having protruding snouts (*Hyla rostrata* and *Pseudacris clarkii*) and strongly inclined anteriorly so as to lie within the prenasal in *Tripriion*. The lingual flange, pars palatina (fig. 17B), of the premaxillary is conspicuous in *Agalychnis*, *Anothea*, *Hemiphractus*, *Pachymedusa*, *Phyllomedusa*, *Smilisca*, the *euthysanota* group of *Ptychohyla*, and many species of *Hyla*, whereas in other *Hyla*, *Acris*, *Phrynohyas*, *Plectrohyla*, *Pseudacris*, *Pternohyla*, *Tripriion*, and the *schmidtorum* group of *Ptychohyla* the pars palatina is inconspicuous. The palatine process is a small posteromedial projection on the pars palatina of the premaxillary (fig. 17B). The palatine process is absent in *Hemiphractus* and inconspicuous in *Acris*, *Pseudacris*, *Tripriion*, and in some species of *Hyla*, *Ptychohyla*, and *Pternohyla*, whereas the process is conspicuous in all other Middle American hylids.

Prenasal: A median bone lying anterior to the maxillaries, premaxillaries, and nasals, and forming the anterior end of the snout in *Tripriion* and the South American *Aparasphenodon* (fig. 17D).

Prevomer: Paired investing bones lying ventral to the solum nasi of the olfactory cap-

sule. The prevomers are variously developed and they articulate anteriorly with the maxillaries and/or the premaxillaries (fig. 17B) in *Anothea*, *Gastrotheca*, *Hemiphractus*, *Pachymedusa*, *Plectrohyla* (except *guatemalensis*), *Phyllomedusa* (except *lemur*), *Smilisca*, *Tripriion*, and in some species of *Hyla*, notably members of the *boans*, *lancasteri*, *miliaria*, and *rubra* (*boulengeri* and *rostrata*) groups, plus *Hyla angustilineata*, *chaneque*, and *thorectes*. Usually the prevomer forms the anterior and medial margins of the internal choanae; however, the lateral processes of the prevomers are reduced so as not to form the margins of the choanae in *Hyla pentheter* and *picadoi*, and in *Hemiphractus* reduced to a slender arcuate bone which likewise does not form the margins of the choanae. The prevomer normally has a transverse or slightly inclined dentigerous process bearing two or more teeth. The processes are greatly reduced in size and lack teeth in some specimens of *Hyla smaragdina*, *smithii*, and *sumichrasti*, and the dentigerous processes are lacking in *Hyla pieta* and *Phyllomedusa lemur*. The dentigerous processes are elongate and angulate in members of the *Hyla boans* and *albomarginata* groups (fig. 19). True teeth are absent, but odontoids are present on the prevomers in *Hemiphractus*.

Pterygoid: Paired, triradiate, supportive bones in the posterolateral part of the skull between the articular region, otic capsule, and suborbital part of the maxillary. The medial ramus of the pterygoid has a bony connection with the prootic in *Anothea*, *Gastrotheca*, *Hemiphractus*, *Pachymedusa*, *Phyllomedusa venusta*, *Phrynohyas*, *Plectrohyla*, *Pseudacris*, some *Agalychnis* and *Ptychohyla*, and in certain species groups of *Hyla* (*albomarginata*, *bistincta*, *boans*, *colymba*, *erythromma*, *lan-*

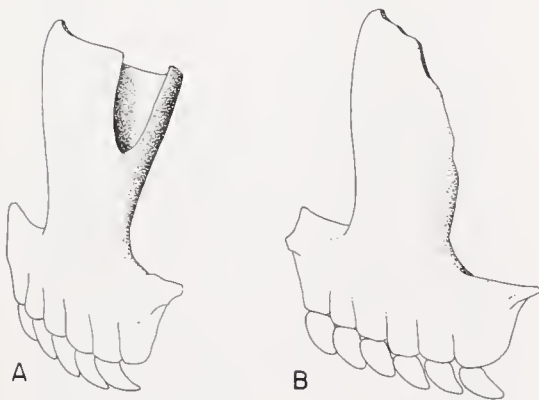


FIG. 18. Premaxillaries. A. Bifid alary process in *Plectrohyla*. B. Single alary process in other genera.

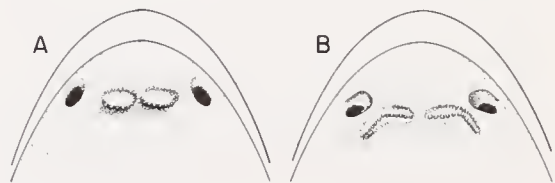


FIG. 19. Dentigerous processes of prevomers as seen in the roof of the mouth. A. Transverse between the choanae. B. Angulate as in the *Hyla boans* and *albomarginata* groups.

casteri, *loquax*, *miliaria*, *pinorum*, *pseudopuma*, *taeniopus*, and *versicolor* groups). The connection is tendinous in *Acris*, *Pternohyla*, *Tripurion*, *Phyllomedusa lemur*, some *Agalychnis* and *Ptychohyla*, and in the other species groups of *Hyla*. In most Middle American hylids, the anterior ramus of the pterygoid articulates with the maxillary at a level near the posterior edge of the orbit, but in some kinds the articulation is at the level of the middle or anterior part of the orbit. The latter condition is typical of *Acris*, *Pseudacris*, *Hemiphractus*, *Plectrohyla avia*, *Pternohyla dentata*, members of the *Hyla eximia* and *versicolor* groups, plus *Hyla angustilineata*, *miliaria*, *pentheter*, *pinorum*, and *siopela*.

Quadratojugal: Small paired bones in the posterior part of the upper jaw. In a fully developed condition the quadratojugal articulates anteriorly with the maxillary; posteriorly the ossification of the quadratojugal invades the cartilage of the quadrate process. Three conditions of the quadratojugal are evident—present and articulating with the maxillary, reduced and not articulating with the maxillary, and absent. The quadratojugal is absent in the *Hyla pictipes* and *sumichrasti* groups, plus *Hyla bromeliacia*, *melanomma*, and *zeteki*. It is reduced or absent in *Ptychohyla*, *Plectrohyla*, and the *Hyla bistincta* and *hazela* groups. The quadratojugal is reduced in the *Hyla leucophyllata*, *microcephala*, *mixomaculata*, *rivularis*, and *parviceps* groups, plus *Hyla arborescens* and *rufoculis*. In all other species of *Hyla* and in the Middle American genera, other than *Ptychohyla* and *Plectrohyla*, the quadratojugal articulates with the maxillary.

Squamosal: Paired, triradiate bones at the posterolateral corners of the skull. The posterior arm and the proximal part of the anterior arm usually articulate with the crista parotica of the prootic, the ventral arm articulates with the quadrate process of the upper jaw. The squamosal lacks a bony articulation with the crista parotica in *Acris*, *Pseudacris*, *Anotheca*, *Plectrohyla ixil* and *matudai*, *Ptychohyla spinipollex*, and in several species groups of *Hyla* (*bistincta*, *bromeliacia*, *eximia*, *godmani*, *leucophyllata*, *microcephala*, *picta*, *salvadorensis*, and *versicolor* groups). In *Pternohyla fodiens* and *Tripurion petasatus*,

the squamosal lacks a bony connection with the crista parotica; instead the squamosal is in broad articulation with the frontoparietal, which is greatly expanded posteriorly and laterally so as to cover the crista parotica. In most hylids, the anterior arm of the squamosal extends anteroventrally from its base for about one-third to one-half of the distance to the maxillary; in these frogs, a tendon connects the anterior arm of the squamosal to the maxillary. In some species in which there is a great proliferation of bone, the anterior arm of the squamosal is in bony contact with the maxillary, thereby forming a complete arch. This condition obtains in eight species of Middle American hylids: *Gastrotheca ceratophrys*, *Hemiphractus panamensis*, *Pternohyla dentata* and *fodiens*, *Smilisca baudinii* and *phacota*, *Tripurion petasatus* and *spatulatus*.

Endochondral Elements

Columella: The cartilaginous and bony rod connecting the tympanum with the inner ear. The only variation noted is that in some species, the columella is expanded distally, whereas in most species, it is of nearly uniform diameter throughout the distal half of its length.

Crista Parotica: The dorsal part of the prootic overlying the columella and extending from the braincase laterally to the squamosal. The major taxonomic feature of the crista parotica is the nature of its connection with the squamosal; this relationship has been discussed under the squamosal.

Exoccipital: A bone forming the posterior end of the braincase posterior to the prootic and around the foramen magnum. In adults, it is fused with the prootic. No variations of taxonomic importance have been noted.

Meckel's Cartilage: The cartilaginous rod of the lower jaw lying medial to the dentary anteriorly and lateral and dorsal to the angulosplenial posteriorly. The cartilage articulates with the cartilaginous quadrate process in the articular region.

Mentomeckelian: Paired small elements in the lower jaw lateral to the mandibular symphysis and articulating with the dentary laterally.

Prootic: The median bone forming the otic capsules and the braincase posterior to

the sphenethmoid and completely fused with the exoccipital in adults. In some species, the prootic is synosteotically united with the sphenethmoid (see discussion under that element).² The nature of the articulation between the median ramus of the pterygoid and the prootic have not been studied thoroughly, even though interspecific differences of potential taxonomic importance probably exist. Comparison of the figures of skulls in the following descriptions of genera and species groups demonstrates differences in the massiveness and width of the otic regions.

Quadrate Process: The cartilaginous process of the articular region articulating with the quadratojugal, ventral arm of the squamosal, posterior ramus of the pterygoid, and Meckel's cartilage. This process can be studied adequately only in serial sections; consequently, it has not been utilized in the taxonomic analysis of characters.

Septomaxillary: Small paired bones lying within the olfactory capsule and possibly of dermal origin. The septomaxillaries are lost in most dried skeletons and appear as free elements in the illustrations of cleared and stained skulls. Trueb (1970a) noted the existence of two architectural types of septomaxillaries. Among the few Middle American species in which this character has been studied, *Phrynohyas* has one type, whereas a second type occurs in *Smilisca baudinii*, *Pternohyla dentata* and *fodiens*, and *Triprion petasatus* and *spatulatus*.

Septum Nasi: The cartilaginous partition between the olfactory capsules. The septum is synchondrotically united with the sphenethmoid posteriorly. In some of those species in which the anterior part of the sphenethmoid is ossified anteriorly, the septum nasi is partly ossified and synosteotically united with the sphenethmoid. This condition is present in *Gastrotheca*, *Hemiphractus*, *Plectrohyla*, *Pternohyla*, *Triprion*, some *Ptychohyla*, and a variety of stream-breeding *Hyla*, including at least some members of the *hazellae*, *miotympanum*, *mixomaculata*, *pseudopuma*, *rivularis*, *taeniopus*, and *zeteki* groups.

A synosteotic unification also is present in *Hyla valancifer* and the *Hyla boans* group.

Sphenethmoid: A median endochondral bone forming the anterior end of the braincase and usually articulating posteriorly with the prootic. The major variation in the sphenethmoid is in the amount of ossification. The sphenethmoid is poorly ossified anteriorly and posteriorly in *Acris* and posteriorly only in *Pseudacris*. The synosteotic relationships of the sphenethmoid anteriorly with the septum nasi have been discussed under the septum nasi. In three of the species (*Hemiphractus panamensis*, *Hyla boans*, and *Plectrohyla guatemalensis*) having synosteotic unification of the sphenethmoid and the septum nasi the sphenethmoid also is synosteotically united with the prootic posteriorly. The same relationship posteriorly is present in *Phyllomedusa venusta*, which does not have synosteotic unification between the sphenethmoid and the septum nasi. In all other species, the sphenethmoid is synchondrotically united with the prootic. Other kinds of variation in the sphenethmoid include the shape, as viewed from the dorsum, of the anterior ossified part. In some groups, the anterior end is broadly truncate and terminates posterior to the nasals; in others it extends anteriorly between or below the nasals and terminates in an acute tip, notched tip, or truncate end. The relationships between the sphenethmoid and nasals were discussed under the latter structure.

Dermal Modifications

Various modifications of the dermal elements occur in hylid frogs; these usually involve and accompany proliferation or expansion of the roofing bones. In most species having a great amount of proliferation of bone, the dermal elements are usually completely or partly involved in integumentary-cranial co-ossification. According to Trueb (1966, p. 572) integumentary-cranial co-ossification involves the deposition of bone in the connective tissue of the lower dermis of the skin. In some species, the co-ossified skull is expanded so as to form a cranial helmet; these are the so-called casque-headed hylids. In Middle America *Pternohyla* and especially *Triprion* have highly modified casqued heads;

² Synosteosis is ossification from two or more centers in the same bone; synchondrosis is the union of two or more elements by cartilage.

in one species in each of those genera a dermal sphenethmoid is present and involved in co-ossification. The bizarre head of *Anotheca spinosa* consists of a skull having many spiny protuberances from the dermal roofing bones, which are co-ossified with the overlying skin. The skull of *Gastrotheca nicefori* is not greatly expanded, but the dermal roofing bones are co-ossified with the skin, and the frontoparietals and squamosals are co-ossified in *Hyla fimbriatembra*.

In *Hemiphractus*, the dermal roofing bones are exostosed and greatly expanded so as to form a triangular helmet, but the skin is not co-ossified with the skull. This most bizarre skull in the hylids is described in detail in the generic account of *Hemiphractus*. The dermal bones of the skull of *Gastrotheca ceratophrys* are expanded and weakly exostosed but not co-ossified.

Osteoderms are present in *Hyla miliaria* and *Phyllomedusa venusta*; in the former they are closely compacted on the head. The skin on the top of the head is immovable, but it is not co-ossified with the roofing bones. The osteoderms make the skin rigid.

Dentition

In all Middle American hylids, teeth are present on the maxillaries and premaxillaries and with the exception of *Hemiphractus* and some small species of *Hyla* (*picta*, and some specimens of *smaragdina*, *smithii*, and *sumichrasti*), teeth are present on the prevomers. Odontoids are present on the dentary and prevomer in *Hemiphractus* and on the parasphenoid in *Triprrion*; these are bony projections and in no way should be confused with the occurrence of true teeth.

In most Middle American hylids, the teeth are spatulate and bifid, or even weakly trifid, but in some of the small species, for example those in the *Hyla leucophyllata* and *microcephala* groups, the teeth are simple and conical. In some species of *Plectrohyla*, notably *avia*, the teeth are long and pointed.

The numbers of maxillary and premaxillary teeth have not been determined except in *Plectrohyla*, a genus in which the number of teeth has customarily been used as a taxonomic character. This negligent dismissal of the number of teeth was done with full knowl-

edge of Goin's (1958) suggestion of the taxonomic importance of the number of teeth. My only excuse is that I was simply too lazy to count all of those minute teeth. However, in the best of herpetological tradition, I did count the number of prevomerine teeth. These data are summarized in Table 3 and show that in general, larger species have more teeth than smaller ones and that larger species in a given species group have more prevomerine teeth than do the smaller species in that group. Further evidence that the number of prevomerine teeth is directly related to the size of the frog is provided by the fact that females of a given species are larger than the males and have on the average more prevomerine teeth.

CHROMOSOMES

Testes were obtained from frogs immediately after they had been drowned in a chlorobutanol "chloretone" solution, and the testes were fixed in a solution composed of 100 per cent methanol, 95 per cent ethanol, acetone, chloroform, and 100 per cent propionic acid, in a ratio by volume of 2:4:1:2:1, respectively. Testicular tissue was squashed and stained with a propiono-orcein stain (see Duellman and Cole, 1965, and Duellman, 1967b, for techniques). Chromosome numbers can be determined by the use of testicular tissue prepared in this manner, but for an analysis of karyotypes, an injection of colchicine into the body cavity prior to killing is necessary (see Cole, 1966, for details).

Hylid frogs are known to have haploid numbers of 11 to 15 chromosomes and diploid numbers of 22 to 30 chromosomes (Duellman, 1967b). The entire range of numbers occurs in the 48 species of Middle American hylids for which data are available (table 4). Insofar as known, the genera *Anotheca*, *Plectrohyla*, *Pteruohyla*, *Ptychohyla*, *Smilisca*, and *Triprrion* have a haploid number of 12 chromosomes. *Agalychnis*, *Pachymedusa*, and *Phyllomedusa* have 13, whereas *Acris* has 11, and *Gastrotheca* has 14. Most Middle American species of *Hyla* have a haploid number of 12 chromosomes, but some have 15.

The data on chromosome numbers is extremely scanty, but even the meager information available presents some interesting points.

TABLE 3

Total Number of Prevomerine Teeth in Middle American Hylid Frogs.
(Means in Parentheses after Observed Ranges)

Species	N	Males Teeth	N	Females Teeth
<i>Acris crepitans</i>	10	4- 8 (6.4)	5	4- 8 (6.8)
<i>Agalychnis annae</i>	35	10-14 (12.0)	5	17-23 (20.2)
<i>Agalychnis calcarifer</i>	2	9-10 (9.5)	1	11
<i>Agalychnis callidryas</i>	26	8-11 (9.7)	7	12-16 (14.0)
<i>Agalychnis litodryas</i>	1	20	0	---
<i>Agalychnis moreletii</i>	25	10-13 (11.2)	6	12-16 (14.2)
<i>Agalychnis saltator</i>	10	7-10 (8.6)	5	9-12 (10.6)
<i>Agalychnis spurrelli</i>	15	14-17 (15.3)	3	16-18 (17.0)
<i>Anotheca spinosa</i>	20	10-19 (12.6)	8	12-19 (12.5)
<i>Gastrotheca ceratophrys</i>	4	14-18 (16.3)	1	17
<i>Gastrotheca nicefori</i>	3	13-16 (14.3)	0	---
<i>Hemiphractus panamensis</i>	11	---	5	---
<i>Hyla altipotens</i>	5	13-18 (15.0)	2	10-12 (11.0)
<i>Hyla angustilineata</i>	12	6-10 (8.3)	3	9-10 (9.3)
<i>Hyla arborescens</i>	23	8-14 (10.8)	4	10-16 (12.6)
<i>Hyla arenicolor</i>	22	9-12 (10.4)	3	10-13 (11.4)
<i>Hyla bistincta</i>	19	6-14 (9.8)	2	10-13 (11.5)
<i>Hyla boans</i>	10	39-53 (48.3)	2	47-52 (49.5)
<i>Hyla bogertae</i>	1	6	1	9
<i>Hyla boulengeri</i>	25	8-17 (13.0)	8	12-19 (15.2)
<i>Hyla bromeliacia</i>	6	6- 8 (6.4)	2	6- 8 (7.0)
<i>Hyla cadaverina</i>	16	4- 7 (6.1)	9	4- 8 (6.4)
<i>Hyla chaneque</i>	25	9-16 (12.6)	6	12-18 (15.2)
<i>Hyla charadricola</i>	10	5-10 (7.6)	3	8-10 (9.0)
<i>Hyla chryses</i>	3	3- 5 (4.3)	1	7
<i>Hyla colymba</i>	6	11-15 (13.0)	3	11-15 (13.3)
<i>Hyla crassa</i>	1	10	1	15
<i>Hyla crepitans</i>	19	20-24 (22.3)	5	25-28 (26.4)
<i>Hyla debilis</i>	9	4- 6 (5.1)	5	6
<i>Hyla dendroscarta</i>	10	6-10 (6.6)	1	8
<i>Hyla ebraccata</i>	25	0- 5 (2.8)	6	4- 7 (5.7)
<i>Hyla echinata</i>	1	14	1	14
<i>Hyla elacochroa</i>	101	3-14 (9.9)	15	9-15 (11.8)
<i>Hyla erythronma</i>	25	8-14 (10.2)	4	14-18 (16.2)
<i>Hyla euphorbiacea</i>	25	5- 9 (7.8)	5	6-10 (8.1)
<i>Hyla eximia</i>	25	6-10 (8.1)	3	6-11 (8.5)
<i>Hyla fimbriembra</i>	0	---	1	16
<i>Hyla godmani</i>	25	8-12 (10.2)	4	7-11 (9.3)
<i>Hyla hazelae</i>	7	8-10 (8.9)	0	---
<i>Hyla lancasteri</i>	23	6- 9 (7.5)	2	12-14 (13.0)
<i>Hyla legleri</i>	18	6- 8 (7.2)	3	8-10 (9.4)
<i>Hyla loquax</i>	25	8-12 (10.3)	4	8-12 (10.0)
<i>Hyla melanomma</i>	19	6- 9 (7.2)	3	6-10 (8.0)
<i>Hyla microcephala</i>	25	4- 7 (6.1)	8	4- 8 (6.3)
<i>Hyla miliaria</i>	4	19-33 (23.8)	1	20
<i>Hyla miotypanum</i>	20	5-11 (8.2)	5	8-14 (10.4)

TABLE 3—(Continued)

Species	N	Males Teeth	N	Females Teeth
<i>Hyla mixe</i>	0	---	2	5- 6 (5.5)
<i>Hyla mixomaculata</i>	3	6-10 (8.2)	2	8-11 (9.5)
<i>Hyla nubicola</i>	3	6- 8 (7.0)	1	8
<i>Hyla pachyderma</i>	1	6	2	8
<i>Hyla pellita</i>	3	6- 8 (7.0)	2	7-10 (8.5)
<i>Hyla pentheter</i>	7	7-11 (8.7)	2	13-15 (14.0)
<i>Hyla phlebodes</i>	25	4- 9 (7.2)	6	5-10 (7.9)
<i>Hyla picadoi</i>	5	4- 6 (5.3)	1	9
<i>Hyla picta</i>	25	0	5	0
<i>Hyla pictipes</i>	25	6-12 (9.0)	6	11-15 (12.7)
<i>Hyla pinorum</i>	5	6- 8 (6.8)	1	8
<i>Hyla plicata</i>	15	8-12 (10.3)	5	10-14 (11.8)
<i>Hyla pseudopuma</i>	30	8-12 (9.6)	11	10-14 (11.6)
<i>Hyla regilla</i>	34	6-11 (7.3)	7	8-12 (10.3)
<i>Hyla rivularis</i>	25	4- 8 (7.1)	6	9-12 (10.8)
<i>Hyla robertmertensi</i>	25	4- 6 (5.1)	5	4- 6 (5.5)
<i>Hyla robertsorum</i>	24	4- 7 (6.0)	5	5- 9 (7.0)
<i>Hyla rosenbergi</i>	18	29-33 (31.0)	7	32-35 (33.8)
<i>Hyla rostrata</i>	28	9-15 (11.2)	1	12
<i>Hyla rubra</i>	17	9-12 (10.6)	4	13-16 (14.2)
<i>Hyla rufoculis</i>	25	4-10 (6.0)	6	7- 9 (8.0)
<i>Hyla rufitela</i>	25	18-23 (21.3)	2	21-23 (22.0)
<i>Hyla salvadorensis</i>	6	6-10 (8.6)	0	---
<i>Hyla sartori</i>	25	6- 8 (7.3)	6	6- 8 (7.5)
<i>Hyla siopela</i>	7	6- 9 (7.9)	5	8- 9 (8.4)
<i>Hyla smaragdina</i>	25	2- 6 (3.8)	1	5
<i>Hyla smithii</i>	25	4- 6 (5.1)	6	5- 7 (6.0)
<i>Hyla staufferi</i>	29	5-11 (7.8)	7	6-11 (8.9)
<i>Hyla subocularis</i>	25	4- 6 (4.8)	6	5- 9 (6.4)
<i>Hyla sumichrasti</i>	23	0- 5 (0.9)	17	0- 6 (1.1)
<i>Hyla taeniopus</i>	18	9-16 (12.7)	8	9-16 (13.3)
<i>Hyla thorectes</i>	20	6-11 (8.3)	2	10-15 (12.5)
<i>Hyla thysanota</i>	0	---	1	21
<i>Hyla tica</i>	21	7-11 (9.0)	6	13-14 (13.3)
<i>Hyla uranochroa</i>	21	6-12 (9.6)	12	8-14 (10.2)
<i>Hyla valancifer</i>	1	18	1	15
<i>Hyla walkeri</i>	20	6-11 (8.2)	3	6-12 (8.7)
<i>Hyla xanthosticta</i>	0	---	1	10
<i>Hyla zeteki</i>	3	6- 8 (7.0)	6	7- 9 (8.0)
<i>Pachymedusa dacnicolor</i>	20	6-11 (8.8)	3	10-12 (11.0)
<i>Phrynobryas venulosa</i>	23	10-24 (15.7)	4	10-27 (17.2)
<i>Phyllomedusa lemur</i>	20	0	2	0
<i>Phyllomedusa venusta</i>	3	10	1	7
<i>Plectrohyla avia</i>	4	2- 6 (4.1)	0	---
<i>Plectrohyla glandulosa</i>	12	2- 6 (4.1)	5	2- 6 (4.3)
<i>Plectrohyla guatemalensis</i>	6	6-10 (7.8)	5	8-12 (9.9)
<i>Plectrohyla hartwegi</i>	3	8-10 (9.0)	0	---
<i>Plectrohyla ixil</i>	22	6-10 (7.7)	4	7-10 (8.6)

TABLE 3—(Continued)

Species	N	Males Teeth	N	Females Teeth
<i>Plectrohyla lacertosa</i>	1	5	0	---
<i>Plectrohyla matudai</i>	8	6-10 (7.4)	3	7-10 (8.3)
<i>Plectrohyla pycnochila</i>	2	6-9 (7.5)	0	---
<i>Plectrohyla quecchi</i>	8	6-8 (7.0)	1	8
<i>Plectrohyla sagorum</i>	15	6-8 (6.9)	4	6-8 (7.2)
<i>Pseudacris clarkii</i>	2	4	0	---
<i>Pternohyla dentata</i>	25	8-12 (10.3)	3	10-12 (10.6)
<i>Pternohyla fodiens</i>	20	8-12 (10.3)	4	11-13 (12.1)
<i>Ptychohyla euthysanota</i>	22	0-6 (4.5)	20	6-18 (9.5)
<i>Ptychohyla ignicolor</i>	38	3-9 (6.1)	7	4-10 (7.3)
<i>Ptychohyla leonhardschultzei</i>	20	6-9 (6.5)	8	7-12 (9.5)
<i>Ptychohyla schmidtorum</i>	65	4-11 (5.3)	13	4-11 (7.9)
<i>Ptychohyla spinipollex</i>	32	3-7 (4.9)	6	6-10 (7.6)
<i>Smilisca baudinii</i>	25	10-17 (14.4)	7	11-18 (15.3)
<i>Smilisca cyanosticta</i>	23	7-21 (13.9)	3	14-22 (17.3)
<i>Smilisca phaeota</i>	10	9-17 (14.0)	10	10-18 (14.6)
<i>Smilisca puma</i>	10	8-14 (10.3)	5	9-15 (11.4)
<i>Smilisca sila</i>	10	9-13 (10.4)	10	10-14 (11.1)
<i>Smilisca sordida</i>	10	8-11 (10.0)	7	8-12 (10.6)
<i>Tripion petasatus</i>	20	8-15 (11.6)	10	14-20 (16.1)
<i>Tripion spatulatus</i>	53	10-15 (12.0)	20	10-16 (13.2)

For example, the species of *Hyla* having a haploid number of 15 chromosomes are members of the *leucophyllata*, *microcephala*, and *parviceps* groups. These three South American groups seem to be closely related on the basis of morphology, tadpoles, and habits. The only other hylid known to have 15 chromosomes is the Papuan *Hyla angiana*. Frogs in the phyllomedusine genera *Agalychnis*, *Pachymedusa*, and *Phyllomedusa* are unique among New World hylids by having 13 chromosomes; this number occurs in Australo-Papuan *Hyla* and *Nyctimystes*. *Acris* is the only hylid known to have 11 chromosomes, and *Gastrotheca* is the only one known to have 14.

VOICE

The advent of high-quality portable tape recorders and sound analyzing equipment within recent years has opened a new field of investigation—bioacoustics. The usefulness of the characteristics of the voice in the taxonomy of frogs has been demonstrated adequately by many workers [see especially Blair (1963b), Bogert (1960), Duellman (1963c),

Duellman and Fouquette (1968), Duellman and Trueb (1966), and Fouquette (1960a)]. The importance of the mating call as an ethological isolating mechanism has been pointed out by several investigators [for recent summaries see Blair (1964), Duellman (1967c), Fouquette (1960b), Littlejohn and Michaud (1959), and Martof and Thompson (1958)].

Kinds of Anuran Calls

Bogert (1960) provided a tentative classification of anuran sounds and thoroughly documented an exhaustive discussion of the kinds of sounds with reference to the biological situations under which the sounds are produced. The following categories of his classification are applicable to Middle American hylids:

Mating Call: The call of the male frog in breeding condition is the most frequently heard and studied kind of call; furthermore, it is this call that is biologically significant as an isolating mechanism. Most species of Middle American hylids produce a mating call; the calls of 76 species are described in the accounts of the species and illustrated on

TABLE 4
Number of Chromosomes
in Middle American Hylids.

Species	Haploid	Diploid
<i>Acris crepitans</i>	11	22
<i>Agalychnis calcarifer</i>	13	...
<i>Agalychnis callidryas</i>	13	26
<i>Anotheca coronata</i>	12	...
<i>Gastrotheca ceratophrys</i>	14	...
<i>Hyla arborescens</i> ^a	12	24
<i>Hyla arenicolor</i>	12	...
<i>Hyla boulengeri</i>	12	...
<i>Hyla chaneque</i>	12	...
<i>Hyla crepitans</i>	12	...
<i>Hyla ebraccata</i>	15	...
<i>Hyla claeochroa</i>	12	...
<i>Hyla erythromma</i>	12	...
<i>Hyla euphorbiacea</i>	12	...
<i>Hyla eximia</i>	12	...
<i>Hyla legleri</i>	12	...
<i>Hyla loquax</i>	12	...
<i>Hyla microcephala</i>	15	...
<i>Hyla pentheter</i> ^b	12	...
<i>Hyla phlebodes</i>	15	...
<i>Hyla pictipes</i>	12	...
<i>Hyla plicata</i> ^c	12	...
<i>Hyla pseudopuma</i>	12	...
<i>Hyla rivularis</i>	12	...
<i>Hyla robertsoni</i>	12	...
<i>Hyla rufoculis</i>	12	...
<i>Hyla rufitela</i>	12	...
<i>Hyla smaragdina</i>	12	...
<i>Hyla smithii</i>	12	...
<i>Hyla staufferi</i>	12	...
<i>Hyla subocularis</i>	15	...
<i>Hyla tica</i>	12	...
<i>Pachymedusa dacnicolor</i>	13	...
<i>Phyllomedusa lemur</i>	13	...
<i>Phyllomedusa venusta</i>	13	...
<i>Plectrohyla ixil</i>	12	...
<i>Plectrohyla sagorum</i>	12	...
<i>Pternohyla fodiens</i>	12	...
<i>Ptychohyla ignicolor</i>	12	24
<i>Ptychohyla leonhardschultzei</i>	12	24
<i>Smilisca baudinii</i>	12	24
<i>Smilisca cyanosticta</i>	12	24
<i>Smilisca phaeota</i>	12	24
<i>Smilisca puma</i>	12	24
<i>Smilisca sila</i>	12	...
<i>Smilisca sordida</i>	12	24
<i>Tripion petasatus</i>	12	24

TABLE 4—(Concluded)

Species	Haploid	Diploid
<i>Tripion spatulatus</i>	12	24

^a Reported as *Hyla hazelae* by Duellman and Cole (1965, p. 141).

^b Reported as *Hyla bistincta* by Duellman and Cole (1965, p. 141).

^c Reported as *Hyla lafrentzi* by Duellman and Cole (1965, p. 141).

plates 12-39. The males of some species of *Hyla* and *Plectrohyla* are mute; vocal slits and a vocal sac are absent. The calls of certain other species, which have vocal slits and a vocal sac, and presumably a mating call, are unknown.

Release Call: The sounds emitted by a male when indiscriminately clasped by another male seemingly are produced by accentuated respiratory movements. Bogert (1960, p. 176) noted that the vibrations on the flanks may be more important than the sounds in eliciting the release of the clasped individual. Release calls are emitted by some males when grasped between the collector's thumb and forefinger. Usually the release call is shorter, more regularly spaced, and pitched at a lower frequency than the mating call of the same species (see plates 37 and 40). Bogert (1960, p. 181) described a release call produced by an unreceptive female *Pachymedusa dacnicolor* when clasped by a male. Charles Myers (1966) noted short grunts produced by several *Hemiphractus panamensis* contained in a back-pack when jostled along a mountain trail; the mating call is not known in this species. Some authors have used the term "warning call" for the calls classified here and by Bogert (1960) as release calls.

Territorial Call: No documented cases of territorial calls are known in hylids, although Greenberg (1942) suggested that the call and pulsating dark throat serve a territorial function in *Acris crepitans*. Many Middle American hylids produce single, often widely spaced notes that essentially are like the note or first of a series of notes in the mating call. These calls, which are known in *Hyla ebraccata*, *H. claeochroa*, *H. rosenbergi*, *Smilisca baudinii*, and *Agalychnis callidryas*, possibly have a territorial function, especially in *Hyla rosen-*

bergi, which emits these calls from high in trees and the normal mating call in shallowly dug basins in swamps or edges of streams. The round of clucking from high in the trees by *Agalychnis callidryas* at dusk might be of territorial significance (see account of that species for details). However, in each of these species, the territorial function is inferred but not demonstrated through observation or experimentation.

Rain Call: The calls emitted by male frogs at areas away from breeding sites are loosely grouped in this category. Usually the notes are radically different from the mating call and frequently these notes are uttered just before or during diurnal showers. For example, the mating call of *Agalychnis callidryas* consists of a single, or sometimes double, note—"chock" repeated at intervals of ten seconds to more than a minute, whereas the rain call consists of a series of short notes, "cluck-cluck-cluck," repeated at intervals of about 0.1 of a second (pl. 30). The rain call of *Hyla eximia* also consists of a series of short notes and is produced by individuals in trees or in bromeliads, whereas the mating call is given only in, or at the edge of, grassy ponds. In those species that have a mating call composed of a single primary note followed by a series of secondary notes and for which a rain call is known, the rain call consists of a single note sounding much like a short primary note. This is the kind of rain call produced by *Hyla ebraccata*, *microcephala*, and *phlebodes*. The rain calls of *Hyla elaeochroa* and *staufferi* are abbreviated versions of a single note in the mating call. I am unaware of rain calls in any of the stream-breeding inhabitants of cloud forests; however, the calling of *Plectrohyla sagorum* from bromeliads by day reported by Taylor and Smith (1945, p. 597) might be so designated, although those authors did not mention differences between those calls and the calls produced by males along streams at night. The function of the rain call is unknown, although Blair (1958) and Bogert (1960) suggested that these calls in some *Hyla* in southeastern United States and in México might have a territorial function.

Distress Call: Bogert (1960, p. 203) used the term distress call for those calls emitted,

usually with the mouth open, when a frog has been seized by a predator. Such calls are well-known in *Rana* and some leptodactylids, and the piercing squall of a *Leptodactylus pentadactylus* held tightly in the hand is legendary among collectors in the American tropics. There have been few reports of distress calls in *Hyla*. Dickerson (1906) mentioned cries of both sexes in *Hyla arenicolor*; Lankes (1928) reported outbursts in the Australian *Hyla caerulea*, and Duellman and Trueb (1966) noted that a female *Smilisca baudinii* emitted a distress call when picked up.

Social Organization in Mating Calls

The social organization in the mating calls seems to have some systematic, as well as ecological importance. Duellman (1967a) reported on social organization in several Neotropical hylids and proposed a classification of social organization in mating calls. The major categories in the classification are: Individual, Non-aggregate, and Aggregate.

In the first category are those species in which there is no aggregation of individuals when calling and no social organization of the calls. *Anothea spinosa*, *Gastrotheca ceratophrys*, and *G. nicefori* seemingly belong in this category. In the former, the eggs are laid in water-filled cavities in trees, whereas in the latter, the eggs are carried by the females. Limited observations on bromeliad-breeders, such as *Hyla bromeliacia*, indicate that there is no breeding aggregation and suggest that there is no organization of calls. Other bromeliad-breeders, such as *Hyla dendrocarta*, *zeteki*, and possibly *picadoi*, also might belong in this category.

In the non-aggregate category are those species that have no aggregation of individuals when calling, but the calls of two or more individuals are organized into duets, trios, or some other sequence. Although this kind of organization is not uncommon in the terrestrial-egg laying *Eleutherodactylus* in humid lowland and montane forests, I cannot definitely assign any Middle American hylids to this category. Perhaps some, or all, of the bromeliad-breeding species of *Hyla* mentioned above belong in this category, but at this time observations on their mating calls

are too fragmentary to determine the presence of organization.

The great majority of Middle American hylids belong in the aggregate category, those species in which individuals congregate at breeding sites and have the calls organized or not. From the limited observations, it has not been possible to demonstrate organization in the mating calls of most of the species, especially the stream-breeders. However, organization is well-developed in the calls of some species, and this organization is one of two basic kinds—completely organized and initially organized. Duellman (1967a, p. 159) described in detail the organization of duets in choruses of *Smilisca baudinii* and of duets, trios, or quartets in *Smilisca puma*. In each of these observations, a dominant individual initiated each successive chorus. A loose organization seems to exist in the calls of the stream-breeding *Smilisca sordida* in which the call is emitted by one individual and picked up by successive individuals along the stream. It is unknown if the same individual initiates successive choruses.

Initial organization is well documented only in *Hyla elaeochroa* in which successive choruses of about 20 individuals were initiated by a definite calling sequence by the same three individuals, after which all individuals commenced calling and organization was no longer apparent (see Duellman, 1967a, p. 161) for details. Initial organization is indicated by limited observations on *Hyla rosenbergi*.

Terminology of Call Structure

Although electronic recording and analysis of anuran calls have been utilized by several workers in the past 15 years, there is a remarkable dearth of detailed commentary on the terminology involved and on the interpretation and methods of measuring various parameters of the calls evident on the audiospectrograms. Blair and Pettus (1954) and Blair (1955) briefly described the use of a spectrographic analyzer, and Fouquette (1960a) and Duellman (1963a) discussed the terminology and techniques of measurement of anuran calls. Borror (1960), Broughton (1963), and Andrieu (1963) described various general terminology and techniques in

bioacoustical research. The methods of recording and analyzing the calls used by me is essentially the same as that employed by other workers, and these methods and kinds of equipment are discussed in a foregoing section on materials and methods. Here I am concerned with the terminology, techniques of measurement, and interpretation of the electrically inscribed marks on the audiospectrogram. The lack of clear definitions of terms and explanation of techniques has had a profound effect of confusing and discouraging novices in this field of research.

The call or call-group is the entire assemblage of sound units produced in a given sequence. In many species, the call consists of a single note, such as in most species of *Agalychnis*, *Phrynohyas*, and many species of *Hyla*, especially the stream-breeding species. In some species, the single note is a long well-pulsed trill; this kind of call is characteristic of *Triprion spatulatus* and members of the *Ptychohyla euthysanota* group. Most species have calls consisting of more than one note. The notes per call-group vary from two or three in many species to several score in frogs such as *Hyla eximia* and *staufferi*. The call rate is the measure of the rate of production of call-groups and is measured in calls per minute.

In those species in which there are two or more notes in the call, the rate in time that notes are produced is called the note repetition rate and is given in the number of notes per minute. In most species, the number of notes can be counted actually during the call or from a recording and the lapsed time measured by means of a stop watch. In those species having extremely short and quickly repeated notes, such as the secondary notes in the *Hyla microcephala* group, it is necessary to measure the time on an audiospectrogram.

A note is any given individual unit of sound, whether the short peep of a centrolenid or the long trill of a toad. On an audiospectrogram, the note is a continuous, or nearly so, darkened area. A note that is continuous and lacks an intermittent pause is said to be monophasic, whereas a note having an intermittent depression in intensity or brief pause is classified as diphasic (fig. 20A). The mono-

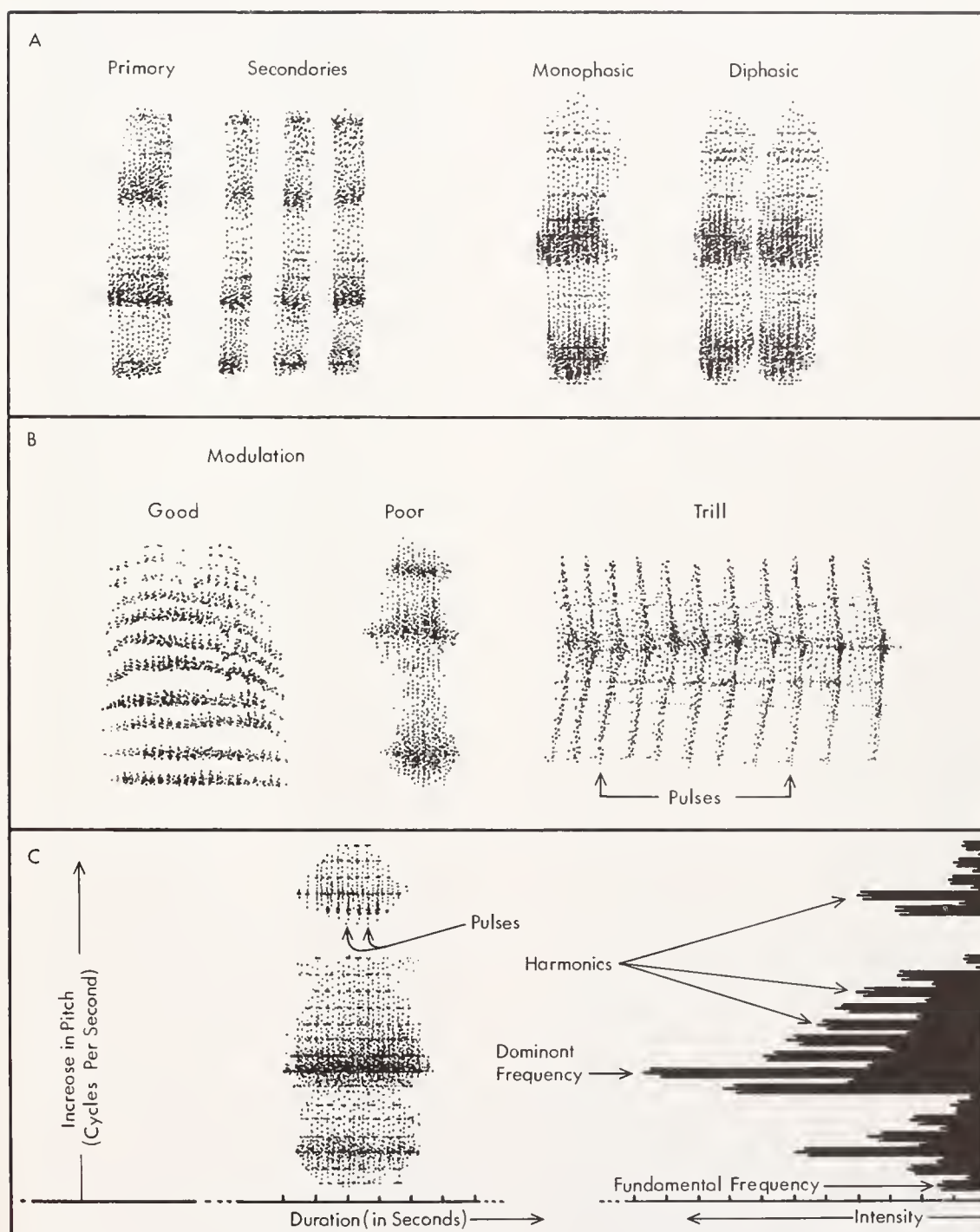


FIG. 20. Diagrammatic representations of sounds as seen on audiospectrograms and sections. A. Kinds of notes. B. Modulation and pulsation. C. Terminology of audio characters.

phasic versus diphasic condition of notes seems to be constant within a species and is a useful criterion in characterizing calls (see audiospectrograms of calls of members of the *Hyla microcephala* group on plates 28 and 29). Some species of frogs produce two kinds of notes that differ in duration (length of note, measured in seconds or parts thereof) and structure (monophasic or diphasic). In most of these species, a long note is followed by one or more shorter notes. In such cases, the long note is called the primary note and the short notes are called secondary notes (fig. 20A). Secondary notes are classified as such only when they are preceded by a primary note. This kind of call is characteristic of members of the *Hyla leucophyllata* and *microcephala* groups. *Hyla melanomma* produces long and short notes (pl. 17), but these are irregularly arranged and consequently do not qualify as primaries and secondaries. Each note has a definite range of frequency (pitch) expressed in cycles per second (cps) or Hertz (htz). In some species, the lowest frequencies approach zero and sounds are produced throughout the frequency spectrum to about 8,000 cycles per second, or even more. In other species, the frequency range is much restricted, usually to the lower frequencies, but in some (*Hyla debilis*, for example) the frequency range is narrow but high. The distribution of the sound (energy) through the frequency spectrum (vertical on audiospectrogram) is a useful systematic character. The distribution of sound is referred to as modulation. In a well-modulated note, the energy is concentrated into a number of narrow bands of frequency (called harmonics and appearing as distinct horizontal lines on audiospectrogram). Opposed to this melodious type of note is the noisy note, in which the sound is spread throughout the frequency spectrum without distinct concentrations as individually defined harmonics (fig. 20B). In the time span of a note, distinct pulsations of sound usually are noticeable; these appear as vertical marks or vertical rows of dots on the audiospectrograms. The pulses can be counted in given notes and in successive notes in order to arrive at the pulse rate, the rate at which pulses are produced. This is given in the number of pulses

per second. In some anurans the notes are long and composed of many distinct pulses that are audible to the human ear (fig. 20B); such notes are usually referred to as trills. Toads of the genus *Bufo* characteristically have a trill. This kind of call is not common in hylids; it is best developed in *Triprion spatulatus* and in members of the *Ptychohyla euthysanota* group (see plates 31 and 34). In some species, particularly some *Agalychnis*, the last one or two pulses in each note are emphasized in intensity.

Various measurements of two parameters of the frequencies of the notes are commonly utilized in studies of anuran calls. The most useful measurements are those of the dominant and fundamental frequencies, both measured in cycles per second (Hertz). The sound emanating from a frog has a spectrum of frequency. In well-modulated notes, the spectrum is divided into distinct harmonics, which are masked, but nevertheless present in poorly modulated notes. That frequency of sound resulting from the air passing over the vocal cords and causing them to vibrate at a frequency primarily dependent on the tension of the vocal cords is the basic (lowest pitched) harmonic and is usually referred to as the fundamental frequency. Each succeeding higher harmonic is a multiple of the basic harmonic. If the fundamental frequency is rather high and is not partially masked, it can be measured directly on the audiospectrogram or section, which is a visual measurement of the relative intensities of the sound throughout the frequency spectrum (fig. 20C). Otherwise, the fundamental frequency can be determined by measuring the distance between several successive adjacent harmonics and dividing the total measurement by the number of harmonics measured.

The frequency of sound resulting from the resonating of the fundamental frequencies or one of its harmonics with greater emphasis than any other frequency is called the dominant frequency. The area of the dominant frequency is the darkest part of the note on the audiospectrogram and is the longest (extended farthest to the left) part on the section (fig. 20C). The dominant frequency usually can be measured with ease directly from the audiospectrogram and more accu-

rately from the section. Otherwise, the dominant frequency can be determined by counting the number of harmonics up to the dominant harmonic and multiplying this number times the fundamental frequency. Acoustically speaking, the dominant frequency is always a multiple of the fundamental frequency, but sufficiently accurate measurement on a scale of 8,800 cycles in a distance of about 100 mm. is not possible. Consequently, the second method is the manner by which to most accurately measure the dominant frequency in most cases. In some species, for example *Smilisca baudinii*, two harmonics are emphasized with nearly the same intensity; in such cases the term dominant frequency has been discarded, and the two emphasized harmonics are called major frequencies.

The fundamental frequency, which is dependent upon the structure and tension of the vocal cords is usually less variable within a given species than is the dominant frequency, which is an expression of the resonating chamber. The vocal sac (resonating chamber) is inflated to various degrees. A partially inflated sac will result in a different dominant frequency than a fully inflated sac. Observations and concomitant recording of certain individuals have resulted in the correlation of a notably lower dominant frequency of a given note with the partial inflation of the vocal sac at the time of the production of that particular note. In well-modulated notes, the harmonics can be counted easily. In these notes it is useful to determine which harmonic is the dominant frequency; the lowest harmonic (fundamental frequency) is counted as number one. A shift upward or downward of one harmonic in the dominant frequency results in considerable variation in the dominant frequency as compared with the fundamental frequency. For example, in a series of recordings of 10 individuals, let us assume that the fundamental frequency varies from 110 to 125 cycles per second. If the dominant frequency is the eighth harmonic, the range of the dominant frequency will vary from 880 to 1000 cycles per second. A shift of one harmonic upward and downward to the dominant fre-

quency in this series would result in a potential frequency range of the dominant frequency from 770 to 1125 cycles per second. This actual and potential variation not withstanding, the position of the dominant frequency still is one of the most important characteristics of the anuran call in systematic studies.

The intensity or loudness of the calls has not been measured. Such measurement is possible by using a sound-level meter at a standard distance from a calling individual. An attempt was made to gather data on intensities in the early part of this study, but was soon abandoned as being impractical in the field. Accurate measurement with a sound-level meter can be obtained only if one frog is calling. Seldom is this the case in the field, for several individuals, if not several species, usually are calling simultaneously. Thus, the sound-level meter measures only the intensity of the sound emanating from an entire chorus. Consequently, objective electronic measurement was forsaken for the subjective human ear, with the result that two generalizations can be made about the loudness of hylid frogs. Larger frogs, such as *Hyla boans*, *H. rosenbergi*, *H. loquax*, *Gastrotheca ceratophrys*, *Smilisca baudinii*, *S. phaeota*, and *Phrynohyas venulosa*, usually have louder calls than do the smaller species. At least, their calls can be heard at a much greater distance than the calls of the smaller species, and in mixed choruses the calls of these species mask those of smaller species. This apparent loudness may be due partly to the lower frequencies that are emphasized in most of these large species. An exception is the relatively soft notes produced by frogs of the genera *Agalychnis*, *Pachymedusa*, and *Phyllomedusa*. The second generalization is that stream-breeders tend to have weaker voices than pond-breeders. In some stream-breeding species, such as members of the *Hyla bistincta* and *mixomaculata* groups and some species of *Plectrohyla*, the voice is absent, whereas in *Ptychohyla*, some *Plectrohyla*, and members of the *Hyla pinorum* and *sumichrasti* groups the voice is soft. In some species, it is barely audible above the sound of flowing water.

Effect of Temperature on Calls

Bellis (1957), Zweifel (1959), Bogert (1960), and Duellman and Trueb (1966) have discussed the effect of temperature on various parameters of the calls of certain anurans. Bellis (1957) noted that in *Pseudacris triseriata* the note repetition rate increased and the duration of the notes decreased with a rise in temperature. Zweifel (1959) analyzed recordings made at temperatures of 16.8° to 25.6° C. of a single *Bombina variegata* and demonstrated that the repetition rate and pitch are positively correlated with temperature, whereas the duration of the call is negatively correlated with temperature. Bogert (1960, p. 299) reported on seven samples of recordings of *Hyla eximia* made at temperatures ranging from 15° to 20° C. at various localities on the Mexican Plateau and noted that the duration of the calls was longer at lower temperatures but that no direct correlation seemed to exist between pulse rate and temperature. Snyder and Jameson (1965) obtained high correlations between temperature and duration of notes and note repetition rate in *Hyla regilla*. Duellman and Trueb (1966, p. 355) noted that in the species of *Smilisca* there exists a positive correlation between pulse rate and temperature and between the level of the fundamental frequency and temperature, whereas no correlations were found between temperature and other parameters of the calls, such as duration and note repetition rate.

During the course of the present study, few conclusive data were obtained on the effect of temperature on calls. This is due principally to the fact that most of the recordings of a given species were obtained within a relatively narrow span of temperature. Two significant exceptions do exist—*Hyla euphorbiacea* and *lanasteri*. Seven individuals of the latter species were recorded at temperatures of 21.7° to 22.0° C. and two were recorded at 16.7° C. Analyses of the audiospectrograms of these recordings showed a positive correlation of the note repetition rate, pulse rate, and level of the dominant frequency with temperature and a negative correlation between the duration of the note and temperature. Analysis of the recordings

of 23 individuals of *Hyla euphorbiacea* at temperatures ranging from 12.5° to 21.5° C. shows a positive correlation of temperature with call rate, note repetition rate, pulse rate and levels of fundamental and dominant frequencies, but a distinct negative correlation between temperature and the duration of the notes; frogs recorded at 12.5° C. produced notes with a duration of 0.08 to 0.11 (mean, 0.098) of a second, whereas those recorded at 21.5° C. produced notes with a duration of 0.04 to 0.05 (mean, 0.047) of a second (see accounts of those species for details). On the basis of most observations, positive correlations between temperature and all parameters of the call, except duration of the notes, seem to exist; duration of the notes apparently is negatively correlated with temperature.

My analysis of 34 recordings of *Hyla eximia* from 10 localities emphasizes Bogert's (1960, p. 299) concern that the variations in calls in that species when compared with the temperature at which the frogs were recorded did not exhibit the kinds of correlations noted by previous workers who had studied other species. The geographic mosaic of variation in calls in *Hyla eximia* points out the fact that many more recordings are needed and that perhaps we are dealing with two or more sibling species (see account of *Hyla eximia*).

Geographic Variation in Mating Calls

Minor variation in certain parameters of the calls of given species are evident in recordings from distant localities. Such geographic variation has been pointed out in *Hyla stauferi* by León (1968) and in *Hyla microcephala*, *robertmertensi*, and *phlebodes* by Duellman and Fouquette (1968). Geographic variation in mating calls is evident in *Hyla ebraccata*, *claeochroa*, *loquax*, *melanomma*, and *uranochroa*, and in *Agalychnis callidryas* (see accounts of these species). Notably because of the absence of large series of recordings of a given species from throughout its range, geographic variation in the mating call of frogs has been largely ignored. An outstanding exception is the sophisticated multivariate analysis of the calls of *Hyla regilla* provided by Snyder and Jameson

(1965), who unfortunately did not take into consideration the size of the individual frogs that were recorded. Future students of geographic variation in the characteristics of calls are obligated to: 1) Record the temperature of the frog immediately after recording the call, 2) Preserve the recorded individual for positive identification and subsequent measurement, 3) Take into account temperature and size in the analysis of geographic variation, and 4) Obtain large series of recordings so that the variation can be treated statistically.

The Mating Call as an Isolating Mechanism

The isolating effects of the mating call in sympatric and synchronic breeding congregations have been discussed and substantiated by numerous authors working with a variety of frogs in North and Middle America, Australia, and South America (see Bogert, 1960, and Blair, 1964, for recent summaries). The mating call as an ethological isolating mechanism has been studied in several Middle American hylids—*Hyla eximia* group by Blair (1960), *Ptychohyla* by Duellman (1963c), *Smilisca* by Duellman and Trueb (1966), *Hyla microcephala* group by Duellman and Fouquette (1968), three sympatric species in Panamá by Fouquette (1960b), and 10 sympatric species in Costa Rica by Duellman (1967c). The conclusions drawn by these authors are supported by data from my analysis of the mating calls of 76 species of Middle American hylids. The single most important conclusion is that sympatric and synchronic breeding species have distinctly different mating calls. In all cases of which I am aware, these differences in calls are distinguishable by the practiced human ear and are clearly recognizable on audiospectrograms.

The frogs of the genus *Ptychohyla* are placed into two species groups on morphological characters and on differences in the mating calls. Members of the *euthysanota* group have a call consisting of a long, well-pulsed note, whereas the call of members of the *schmidtorum* group consists of a series of short notes. Throughout most of the range of the genus sympatric species pairs breed side by side along streams; in each case the

pairs are made up of one species from each group.

Duellman and Trueb (1966) noted that the calls of the allopatric species *Smilisca puma* and *sila* are not greatly different, whereas *Smilisca sordida* has a distinctively different call and occurs sympatrically with *puma* and *sila*. Duellman and Fouquette (1968) noted that of the four species in the *Hyla microcephala* group, the most divergence in mating calls occurs in the only two sympatric species in the group—*Hyla microcephala* and *phlebodes*.

In the Mexican *Hyla eximia* group, the calls of the geographically adjacent *Hyla eximia* (long series of notes) and *Hyla euphorbiacea* (short series of short notes) are distinctly different. The calls of the widely allopatric *Hyla euphorbiacea* and *walkeri* are very much alike. *Hyla plicata* occurs sympatrically with *eximia* and differs from *eximia* by having a long, trilled note. In the Middle American members of the *Hyla boans* group, the ranges of *boans* and *crepitans* are mutually exclusive, whereas *rosenbergi* occurs sympatrically with both *boans* and *crepitans*. Although the number of notes in each call-group, the duration of the notes, and the level of the fundamental frequency are different between *boans* and *crepitans* other parameters of the calls are similar. On the other hand, the call of *rosenbergi*, although structurally the same as in the other members of the group, is notably different by having a much lower dominant frequency (272 cycles per second, as compared with 869 in *boans* and 1107 in *crepitans*).

Isolating mechanisms sometimes fail; this is strongly suggested by an individual frog obtained at Bejuco, Panamá Province, Panamá, by Richard G. Zweifel in 1962. Morphologically, the frog is intermediate between *Hyla crepitans* and *rosenbergi*. A recording obtained of the call of another individual at the same time shows that the call is intermediate in some parameters and different from both supposed parental species in other characteristics. Mecham (1960) documented natural hybridization between *Hyla cinerea* and *gratiosa* in Alabama.

Fouquette (1960b) studied the calls and mating behavior of *Hyla ebraccata*, *micro-*

cephala, and *phlebodes* in the Canal Zone and concluded that the mating call seems to be the primary isolating mechanism operating to prevent interbreeding of the three species studied. He provided evidence that the three species have calls that are qualitatively and quantitatively different, and he assumed that females discriminate and respond only to the call of their own species. Fouquette's assumption that the females can discriminate between the calls of their own and other species seemingly is well founded. Experimental tests by Martof and Thompson (1958), Littlejohn and Michaud (1959), and Snyder and Jameson (1965) showed that in various species of *Hyla* and *Pseudacris*, the gravid females respond positively to the calls of their own species and generally are indifferent to the calls of other species. Duellman (1967c) studied courtship behavior of 10 species of hylids at a pond in Costa Rica and concluded: "whereas mechanical isolation between some species is obvious, principally due to great differences in size, the more important isolating mechanisms are differences in behavior. Although each species has characteristic calling and oviposition sites, these sites are not necessarily exclusive. Consequently, these aspects of courtship and mating cannot be considered as primary mechanisms operating to prevent mismatings." These conclusions are not contradicted by extensive observations on other associations of both pond- and stream-breeding frogs. All existing evidence points to the mating call as an important ethological isolating mechanism that is the result of selective pressures to insure the attraction of females of the species and as an aid in preventing mismatings and the consequent wastage of gametes.

Systematic Importance of Mating Calls

Most of the studies on mating calls of anurans have been concerned with call differentiation and interspecific isolating effects. The use of the mating call in systematic studies has been more limited. Blair (1963a), Bogert (1962), and Porter (1964 and 1966) reported on calls of *Bufo*. Littlejohn (1959) utilized mating calls in his studies on the Australian leptodactylids of the genus *Crinia*. The mating call has been utilized as a system-

atic tool in *Agalychnis* (Duellman, 1963d), *Ptychohyla* (Duellman, 1963c), *Smilisca* (Duellman and Trueb, 1966), and in the *Hyla microcephala* group (Duellman and Fouquette, 1968). Knowledge of differences in mating calls has been useful in recognizing that certain allopatric populations are different species, such as in *Hyla arenicolor* and *cadaverina* (Gorman, 1960), and the lack of differences in mating calls in certain polymorphic species, such as *Hyla ebraccata* and *weyeri*, have aided in the determination of the existence of only one species (Duellman, 1966b).

Despite the great amount of work that has been done on anuran mating calls the only existing treatment of mating call along with morphological characters in a large natural group of species is Schiøtz's (1967) monograph of the West African frogs of the family Rhacophoridae. Schiøtz summarized his work on the mating calls as follows:

"Seen as a unit, the voices of the West African Amphibia can be expected to be subjected to the following, partly alternative rules:

I. That the voices are in accordance with the morphological characters supporting the taxonomy, so that the species within a genus have characters in common, not shared with species from other genera, and members of genera in one family have characters in common, not shared with genera in other families.

II. That the voices, being adaptive characters, are influenced by the habitat occupied by the species, or by the complex of exterior factors, physical and biological, characteristic for a habitat. This will imply that members of the same breeding fauna have voices with common characters.

III. That it is essential that the voice of a certain species can be distinguished from all other voices it is heard together with, *i.e.* voices of other members of the same breeding fauna, excepting geographically non-overlapping species. This rule would mean that there is the greatest possible diversity in the voices from one breeding fauna.

IV. Finally, the possibility exists that the voices have developed according to other rules than those mentioned in I-III. In this case, no correlation should be found between

the voices and the taxonomy or the habitat preference."

Schiøtz is to be envied of the vocalizations of West African rhacophorids; the nature of the generic and familial characters of mating calls that he discusses at length (1967, pp. 294-295) is substantially different, at least at the generic level, in Middle American hylids. Although members of some genera, such as *Pseudacris*, *Phrynohyas*, and some species groups in *Hyla* and *Ptychohyla* have several call parameters in common with other members of the same taxonomic group, an equal number of groups are not so readily characterized. For example, the trill-like call of *Hyla pictipes* is not greatly different from the trills of members of the *Ptychohyla euthysanota* group, and the series of nasal notes produced by *Hyla eximia* is more like the call of *Hyla staufferi* and certain other members of the predominantly South American *Hyla rubra* group than it is like the calls of other members of the North American *Hyla eximia* group.

Schiøtz's second rule does not seem to apply to Middle American hylids, except in the most general way. I have serious doubts about the influence of the habitat on the vocalizations, except for the tendency to have a weak voice or no voice in certain stream-breeding frogs. The various kinds of voices known in Middle American hylids show no definitive correlation with habitat. Frogs having a long, well-pulsed note call from streams and ponds. Calls of single or multiple notes are emitted by frogs that call from trees or low herbaceous vegetation, along streams or around ponds.

I have discussed previously the divergence in calls in sympatric species, a point made by Schiøtz in his third rule. Thus, it is obvious that to the taxonomist the voice is a valid recognition character. The trained ear can discern anuran species as readily as the ornithologist can identify birds on the basis of their songs.

In each of the species accounts, the mating call, when known, is described in general terms, and the parameters of the vocal factors are given; these are summarized in table 5. In simple terms, the calls of Middle American hylids can be placed in three groups: calls

consisting of one note (28 species), call groups comprised of a series of like notes (40 species), and call-groups made up of a primary note followed by a series of secondary notes (8 species). Usually groups of closely related species fall into only one group, but exceptions do occur. For example, of the six species in *Smilisca*, three are in the first category, one in the second, and two in the third, and in the *Hyla rubra* group two species are in the first category and three are in the second. On the other hand, all species of *Agalychnis* are in the first category, all members of the *Hyla rivularis*, *boans*, *uranochroa*, and *miotympanum* groups are in the second category, and all members of the *Hyla microcephala* group are in the third category.

Within groups of closely related species, the kinds of differences between species are variable. Although minor differences in the level of the fundamental and dominant frequencies are consistent in the *Hyla microcephala* group, the most striking difference is in the phase of the notes—monophasic versus diphasic structure of primary and secondary notes. In the *Hyla rivularis* group, the primary interspecific differences are in note repetition rate and the level of the dominant frequency, whereas in *Smilisca*, the duration and pulse rate are significant factors. Thus, it seems that no general rule can be applied regarding significance of vocal factors; each group of species has its own combination of characters and kinds of interspecific differences.

Although similarities in mating calls between two or more species might be an indication of relationships among those species, such conclusions can be justified only when other criteria (morphology, development, behavior) lend support. Frogs have rather limited vocal abilities; consequently, the occurrence of similar kinds of calls in widely allopatric species is to be expected. The disregard of morphological characters by Blair (1959 and 1960) resulted in his placing of *Smilisca baudinii* in the *Hyla versicolor* group and *Hyla staufferi* in the *Hyla eximia* group, both solely on the basis of call structure. Throughout the course of the present study, I have relied on the mating calls as an aid in the identification of sympatric species and

TABLE 5
 Characteristics of the Mating Calls of Middle American Hylid Frogs.
 Values Given Are Means

Species	N	Notes per Call Group	Call Rate (min.)	Note Repetition Rate (min.)	Duration (sec.)	Pulse Rate (sec.)	Fundamental Frequency (cps)	Dominant Frequency (cps)
One Note:								
<i>Agalychnis annae</i>	13	1	0.5	0.31	42	161	1165
<i>Agalychnis callidryas</i> ^a	25	1	2.0	0.16	189	182	1975
<i>Agalychnis litodryas</i>	1	1	3.0	0.15	105	104	1664
<i>Agalychnis morletii</i>	8	1	0.3	0.13	58	172	1171
<i>Agalychnis saltator</i> ^a	2	1	0.5	0.10	108	120	1867
<i>Agalychnis spurrelli</i>	2	1	4.0	0.37	75	94	568
<i>Gastrotheca ceratophrys</i>	1	1	0.1	0.08	800	800
<i>Hyla boulengeri</i>	8	1	0.5	0.35	101	71	1611
<i>Hyla chaneque</i>	5	1	1.0	0.59	59	1674
<i>Hyla erythromma</i>	1	1	1.5	0.62	26	87	2266
<i>Hyla lancasteri</i>	9	1	13.0	0.07	150	1525
<i>Hyla legleri</i>	8	1	14.0	0.29	108	149	1274
<i>Hyla pictipes</i>	7	1	1.0	0.32	123	2591
<i>Hyla plicata</i>	3	1	40.0	0.63	90	96	1495
<i>Hyla rostrata</i>	7	1	0.5	0.69	51	56	918
<i>Hyla subocularis</i>	2	1	4.0	0.53	43	2200
<i>Pachymedusa dacnicolor</i>	6	1	1.0	0.23	159	153	1727
<i>Phrynohyas venulosa</i>	7	1	47.0	0.30	161	159	1622
<i>Phyllomedusa lemur</i>	2	1	2.0	0.25	108	114	2396
<i>Plectrohyla ixil</i>	2	1	7.0	0.22	200	700	2100
<i>Ptychohyla euthysanota</i>	7	1	15.0	0.62	96	3100
<i>Ptychohyla leonhardschultzei</i>	2	1	1.0	0.76	77	2750
<i>Ptychohyla spinipollex</i>	1	1	0.5	0.46	147	4300
<i>Smilisca cyanosticta</i> ^a	10	1	3.0	0.38	147	145	841
<i>Smilisca phaeota</i> ^a	10	1	2.0	0.31	116	143	372
<i>Smilisca sordida</i> ^a	19	1	0.4	0.29	105	123	1216
<i>Triprrion petasatus</i>	7	1	48.0	0.30	85	287	2096
<i>Triprrion spatulatus</i>	6	1	13.0	0.85	99	103	1745
Series of Short Notes:								
<i>Acris crepitans</i>	1	many	120	0.05	70	175	3150
<i>Anotheca spinosa</i>	1	128	137	0.10	220	540	540
<i>Hyla angustilineata</i>	1	2	1	2	0.10	90	87	1653
<i>Hyla arboreascendens</i>	1	19	1	69	0.25	80	74	2072
<i>Hyla arenicolor</i>	13	29	0.64	26	102	2329
<i>Hyla boans</i>	3	6	69	0.26	107	114	869
<i>Hyla bromeliacia</i>	1	5	1	60	0.14	195	135	3100

TABLE 5—(Continued)

<i>Hyla cadaverina</i>	4	—	—	47	0.14	131	132	2073
<i>Hyla colymba</i>	3	58	—	179	0.05	—	1800	3600
<i>Hyla crepitans</i>	3	4	—	88	0.04	110	182	1107
<i>Hyla debilis</i>	8	6	2.0	12	0.01	—	—	5235
<i>Hyla elacochroa</i>	15	19	—	—	0.17	42	57	1499
<i>Hyla euphorbiacea</i>	23	7	25.0	664	0.06	103	108	2168
<i>Hyla eximia</i>	34	—	—	76	0.23	82	104	2058
<i>Hyla godmani</i>	7	—	—	18	0.17	60	—	2920
<i>Hyla hazelae</i>	2	—	—	26	0.06	130	—	1825
<i>Hyla loquax</i>	9	—	—	31	0.10	129	—	2323
<i>Hyla melanomma</i> ^b	8	4	3.0	72	0.07	277	170	2383
<i>Hyla miotympanum</i>	27	7	5.0	65	0.10	—	—	2415
<i>Hyla picta</i>	11	—	—	64	0.04	53	2661	2661
<i>Hyla pseudopuma</i>	2	3	4.0	45	0.03	85	69	956
<i>Hyla regilla</i>	1	—	—	30	0.10	—	121	2420
<i>Hyla rivularis</i>	7	34	3.0	102	0.02	—	—	2420
<i>Hyla rosenbergi</i>	5	3	—	129	0.06	50	136	272
<i>Hyla rubra</i>	5	3	—	—	0.13	63	61	1581
<i>Hyla ruficulis</i>	2	3	10.0	—	0.06	—	87	2320
<i>Hyla rufitela</i>	3	14	—	38	0.05	—	400	1600
<i>Hyla salvadorensis</i>	4	4	—	—	0.08	—	—	2345
<i>Hyla smithii</i>	3	—	—	68	0.03	36	1033	2066
<i>Hyla stauferi</i>	25	19	—	—	0.16	120	108	1817
<i>Hyla sumichrasti</i>	3	24	—	154	0.20	71	94	1877
<i>Hyla thorectes</i>	3	15	—	24	0.21	67	126	2062
<i>Hyla tica</i>	5	4	37.0	148	0.02	—	—	2228
<i>Hyla uranochroa</i>	4	—	—	148	0.04	260	992	1969
<i>Hyla walkeri</i>	4	5	39.0	1090	0.03	120	158	1910
<i>Pseudacris clarkii</i>	4	—	—	144	0.17	93	78	2554
<i>Pternohyla fodiens</i>	9	—	—	95	0.25	122	126	2230
<i>Ptychohyla ignicolor</i>	4	8	—	420	0.08	126	—	3500
<i>Ptychohyla schmidtorum</i>	4	6	—	360	0.65	105	—	3400
<i>Smilisca baudinii</i>	20	8	4.0	222	0.11	174	166	351

Primary and Secondary Notes:^c

<i>Gastrotheca nicefori</i>	1	1+2—6	12.0	240	0.55	85	87	957
<i>Hyla ebraccata</i>	43	1+2—5	—	311	0.16	97	—	2504
<i>Hyla microcephala</i>	91	1+0—18	—	268	0.12	163	213	5710
<i>Hyla phlebodes</i>	34	1+0—28	—	284	0.11	152	148	3578
<i>Hyla robertmertensi</i>	25	1+0—28	—	418	0.09	149	162	5388
<i>Hyla sartori</i>	10	1+0—23	—	434	0.08	149	126	3217
<i>Smilisca puma</i>	28	1+1—10	3.0	720	0.13	208	145	743
<i>Smilisca sila</i>	15	1+1—6	6.0	600	0.16	108	103	899

^a Call sometimes is comprised of two notes.^b Long notes also produced; not included here.^c Number of secondary notes given after plus sign; note repetition rate is for secondary notes; other parameters are for primary notes.

as evidence to support ideas of relationships based on morphological characters.

Evolutionary trends in mating calls are not clearly evident. So much of the differentiation of calls seems to be related to selective pressure by the vocalizations of sympatric species I am unsure that it is possible to determine evolutionary trends in any more than a very general way. The primitive type of call probably consisted of a single note, which was drawn out into a trill in some species and fragmented into a series of notes or merely just repeated at a rapid rate in other species, thereby giving rise to calls comprised of a series of like notes. Further modification could have resulted in the development of a longer primary note and a series of shorter secondary notes.

In conclusion, it is evident that the mating calls are just as useful in recognition by taxonomists as by the frogs themselves. However, the various parameters of the mating calls represent only one of several sets of characters possessed by species and should not be used to the exclusion of other characters.

TAXONOMIC CRITERIA IN HYLID FROGS

Each group of animals is studied in somewhat different ways. The kinds of characters used and the importance of these characters in the determination of relationships reflects the judgment of the taxonomists working on the groups. All too often, taxonomic treatises contain no statements by the author about his evaluation of the characters used. Of course, I would be remiss if I did not mention the methodology suggested by the students of numerical taxonomy who give an equal weight to many characters and allow a computer to determine the relationships of the taxa. However, I believe that on the basis of my familiarity with the animals in life, as well as with the characters exhibited by the preserved specimens, I can justifiably give more weight to some characters than to others and also determine that certain characters are significant in one group and meaningless in others. The conceptual bases for my taxonomic arrangement are discussed below.

The Species Concept

I completely agree with Simpson (1961, p. 150) that the only acceptable definition of species category must have a meaningful relation to evolution and further agree with Simpson on the acceptability of Mayr's (1942) definition: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." The acceptance of this definition implies genetic differences in populations, but does not tell us how these differences are expressed. We assume that each species exists as an entity in nature and base our hierarchy of classification on the reality of the species (Burma, 1954). However, we examine phenotypes and draw conclusions that can be proved only by determination of the genotypes. Thus, judgments regarding the nature of the species in hylid frogs have been made with the concepts of genetic and evolutionary species in mind, but the practical bases for determinations have been phenotypic expressions (morphological and behavioral) of supposed genetic traits.

The definition of species with which I am thoroughly familiar in life and for which I have available a variety of material (preserved adults, skeletons, tadpoles, and recordings of mating calls) is relatively easy, except in certain cases of vicariant populations. The demonstration of geographical, and especially ecological, sympatry is a criterion which I have used to determine the specific status of certain taxa. In most cases, this evidence has been further supplemented by differences in mating calls or larval morphology, when the adults were exceedingly similar. Thus, the specific nature of several species pairs (*Hyla boulengeri* and *rostrata*, *Hyla microcephala underwoodi* and *H. phlebodes*, *Smilisca sila* and *sordida*, as examples) have been ascertained.

The criteria for species are not consistent throughout the taxonomic treatment for two reasons. First, characters that are useful in certain groups are either absent, invariable, or so variable as to be meaningless in others. For example, the tadpoles of the species of *Plectrohyla* and *Ptychohyla* possess characters or combinations of characters by which the tadpoles of the different species can be

identified readily. Contrariwise, the tadpoles of the species *Agalychnis* are so nearly alike that identification is exceedingly difficult or impossible. The mating calls of some species are very diagnostic; in others, the calls are little different from other allopatric species. In some groups of species, size and proportions are useful in identification, whereas in others, such as the members of the *Hyla microcephala* group, each proportion seems to vary independently in each sample. Obviously, the characteristics of the mating call cannot be relied upon in those groups in which the species are mute (*Hyla bistincta* and *mixomaculata* groups and some species of *Plectrohyla*). The second reason for inconsistency is the absence of certain kinds of data. The lack of tadpoles and recordings of the five species in the *Hyla miliaria* group necessitated the definition of those species solely on the basis of the morphological characters of the adults. If all of the information were available for all of the species, more satisfactory and universal sets of criteria could be used.

Despite the approach to the problem of defining species on the conceptual basis of the genetic species, it has been necessary to resort to the practical morphological methods in most instances. The utilization of the degree of differences has been necessary in dealing with many allopatric populations. Thus, some populations are recognized as species distinct from other populations solely because the differences in certain morphological characters were much greater between the samples than within samples.

In conclusion, I emphasize that my tendency is to lump, rather than to split. Some of my colleagues probably have come to feel that I have demonstrated otherwise in my naming of several new species in the past few years, but if I had been basing my ideas on few preserved specimens instead of biological populations, the number would have been many more. This is evidenced by my early study on *Phrynohyas* (1956a) based only on preserved material, in which I accounted for five species in Middle America, whereas now I recognize only one.

Intraspecific Variation and Subspecies

The treatment of intraspecific variation, especially geographically, often invokes emotional reactions from many taxonomists. The splitters would recognize each variant population taxonomically, whereas the lumpers would abandon the use of the concept. I have tried to take a reasonable approach to the subspecies and in general have been extremely conservative. Detailed statistical analyses of many characters will, and have in some cases, demonstrate statistical differences in populations, which could be, and have been in some cases, named.

The taxonomic recognition of populations exhibiting minor differences often obscures many biological facts and usually contributes nothing to our understanding of the nature of variation and the correlation of variation with environmental changes, if any. The most remarkable example of variation in a Middle American hylid is that displayed by *Hyla lancasteri*, which is so distinctly different on the upper slopes of Cerro Pando from elsewhere in the range that the population there might even have been accorded generic status. Trueb (1968a) clearly demonstrated that the fantastic "spiny frog" on Cerro Pando is an altitudinal variant of the rather nondescript *Hyla lancasteri* on the lowlands. The altitudinal gradient in structure, color, and behavior of the frog correlates with environmental gradients. This extreme case has caused me to wonder if some other distinctive allopatric species might actually be the ends of clines.

I have recognized few subspecies among Middle American hylids. My criteria for subspecies have been: 1) Allopatric adjacent (or probably adjacent) ranges. 2) Distinct morphological differences that are constant, or nearly so, within each population. 3) Like mating calls. 4) Narrow areas of intergradation usually associated with a physical barrier or ecotone. Criteria such as these are applicable to species in which certain populations have undergone differentiation in response to isolation or to differences in environments. Thus, the recognition of two subspecies each in *Hyla melanomma*, *H. pseudopuma*, *Ptychohyla euthysanota*, and *P. schmidtorum* is based in part on the separation of the subspecies by

a physical barrier, which provides ecological conditions unsuitable for the species. The ranges of the subspecies of *Hyla staufferi* and *Triprrion spatulatus* are separated by ecological barriers, in each case a humid forested area between the inhabited drier areas. The subspecies of *Hyla microcephala* meet and intergrade in an area of transition between wet and dry forest.

Care has been exercised not to place certain allopatric populations in one species when only minor differences in structure and color are evident, if information on the mating calls and life histories were not available. On the basis of adult frogs alone, one might consider *Hyla euphorbiacea* to be a subspecies of *Hyla eximia*, but differences in the mating calls strongly indicate that the two narrowly separated populations are species. The mating calls provide good evidence for the determination of distinctness of allopatric populations. The first clue to the relationships of *Hyla melanomma* and *bivocata* was provided by recordings of the calls.

In some instances, my attempts at consistency have lapsed, due mostly to lack of data. While I can demonstrate significant differences in the mating calls of *Hyla eximia* and *euphorbiacea*, I have no data on the call of the population of *eximia* formerly assigned to *arboricola*, which, because of its allopatric distribution and structural similarity, I regard as the same as *eximia*.

Species Groups and Genera

The supraspecific groupings of hyliid frogs are inherently inconsistent. Within the family some 30 genera are currently recognized, but about three-fourths of the approximately 500 species are placed in the genus *Hyla*. Widely divergent species or groups of species have been segregated from the genus *Hyla*; these include the bizarre casque-headed genera, such as *Aparasphenodon*, *Pternohyla*, and *Triprrion*, other genera that are distinctive in osteological features (*Anotheca* and *Hemiphractus*), and some that have peculiar life histories, such as exhibited by *Cryptobatrachus* and *Gastrotheca*. The nature of the vocal sacs has been used in separate *Smilisca* and *Phrynohyas* from *Hyla*, whereas progressive ossification of the skull and the develop-

ment of a cranial casque provide the generic characters to separate *Osteocephalus* and *Trachycephalus* from *Phrynohyas*. Other genera are recognized on more subtle characters. For example, the genus *Ptychohyla* differs from *Hyla* solely by the presence of large ventrolateral glands in the males. The genus *Plectrohyla* has been recognized formerly only on the basis of the absence of a quadratojugal and the presence of an enlarged, protruding prepollical spine. The absence of a quadratojugal is characteristic of many species of *Hyla*, and members of several species groups of *Hyla* have a protruding prepollical spine.

I have taken a conservative view of genera and have recognized generically only those groups (genus *Hyla* is an exception) that assuredly represent a single phyletic line and that display a unique combination of morphological and behavioral traits, plus a probable paleogeographic history that has been the basis for the evolutionary separation of the group. For the most part, I have followed the currently accepted generic groupings, principally because the key to many phyletic lines must await the accumulation of data on some of the presently poorly known groups in South America. In this regard a treatment of Middle American hyliid frogs cannot take into consideration the phylogenetic relationships of the casque-headed and non-casque-headed frogs currently assigned to the genus *Gastrotheca*, represented by *nieefori* and *ceratophrys*, respectively, in Central America and by many species in South America. Likewise, the two Central American species of *Phyllomedusa* (*lemur* and *venusta*) represent extremes of variation within the genus, which has a wide array of species in South America.

In contrast to some of the weakly defined genera some species groups in the genus *Hyla* are widely divergent. For example, the large fringe-limbed *Hyla* with heavily ossified skulls are in marked contrast to the small species in the *Hyla microcephala* group, which have weakly ossified skulls. Generic recognition of some of these diverse groups is possible on morphological basis, but again the lack of knowledge about South American relatives precludes an understanding of the

entire range of variation within the groups and their relationships with other groups.

The definition of species groups is based on the premise that all of the members of a given group have a common ancestor. Species groups, like genera, are not necessarily defined on corresponding sets of characters. For example, in some of the lowland groups of *Hyla* that are principally South American in distribution, the larval characters are not heavily relied upon to show affinities of the species, whereas some of the principal characters in the definition of groups of stream-breeding hylids in México are those of the tadpoles. It may seem to some taxonomists that I have overly split the species groups, even to the recognition of "groups" that contain only one species. This has been done in cases where the inclusion of a certain species in another group would result in the breakdown of the group characters. Moreover, and more importantly, each species group is considered to represent one phyletic line. Naturally, the supposed points of divergence of various phyletic lines is variable; consequently, the inclusion of several phyletic lines in one large group is possible, but not practical for our purpose. Thus, where I recognize the *pictipes*, *rivularis*, *salvadorensis*, and *uranochroa* groups in the genus *Hyla* in Central America and consider all of these to be related to one another, the divergent adaptations in the various groups are such that definition of a composite group is nearly impossible.

IDENTIFICATION OF MIDDLE AMERICAN HYLID FROGS

The construction of keys to the identification of the Middle American hylids has been a difficult task, one in which I feel that I have been only moderately successful. Ideally, a good key will permit the identification of specimens of either sex to species or subspecies; such is not the case with the following keys, because a person unfamiliar with the general appearance of frogs of the genera *Ptychohyla* and *Smilisca* will not be able to allocate females to their proper genus. Juveniles of most species are difficult or impossible to identify by means of the keys, which have been constructed for adult males.

One key is provided to the genera and one each for those genera in Middle America represented by two or more species; thus, there are no generic keys for *Acris*, *Anotheca*, *Hemiphractus*, *Pachymedusa*, *Phrynohyas*, and *Pseudacris*. The generic keys are in alphabetical order by the generic name. A single key to the 73 species of Middle American *Hyla* proved to be unworkable. Consequently, three keys to the species in three geographic regions are presented.

The keys are designed to be used in conjunction with text figures 3-11, to which references are given in the keys. The colored plates are especially helpful in identifying many species and should be used with the diagnoses and descriptions. As a final commentary on the use of any one of the keys, I quote Stuart (1955, p. 10): "... the worker who knows what species he has before him should experience few difficulties in its use."

KEY TO THE GENERA OF MIDDLE AMERICAN HYLID FROGS

1. Pupil vertically elliptical (fig. 5A); dorsum usually bright green in life (blue in preservative) 2
Pupil horizontally elliptical (fig. 5B); dorsum variable 4
2. No webbing on hands and feet; palpebral membrane clear ... *Phyllomedusa*
Some webbing on hands and feet; palpebral membrane usually reticulated (fig. 5B) 3
3. Head shallow, depth less than 40 per cent of length; discs large; fingers at least one-half webbed; iris red or orange and palpebral membrane reticulated (iris yellow and palpebral membrane clear in *calcarifer*)
..... *Agalychnis*
Head deep, depth more than 50 per cent of length; fingers webbed basally; iris gold with black reticulations; palpebral membrane reticulated *Pachymedusa*
4. Skin co-ossified with skull; extensive bony labial flanges present; fingers no more than one-half webbed 5
Skin not co-ossified with skull, or, if

- so, bony labial flanges absent; webbing variable 6
5. A prenasal bone (fig. 17D) present; labial shelf greatly expanded laterally; body moderately slender; head much longer than wide *Triprior*
Prenasal bone absent; labial shelf moderately expanded laterally; body short, squat, toad-like; head only slightly longer than wide *Pternohyla*
6. Fingers long, essentially unwebbed, lacking nuptial excrescences in males; head as broad as long 7
Fingers not long and lacking webs, or, if so, males having nuptial excrescences or size small (less than 30 mm. in snout-vent length); head variable 9
7. A fleshy proboscis (fig. 4I); head triangular in dorsal view *Hemiphractus*
No fleshy proboscis; head not triangular in dorsal view 8
8. Skin co-ossified with skull; long dorsally directed spines on periphery of roofing bones of skull; no brood pouch in females *Anothea*
Skin co-ossified or not; no spines on skull; a brood pouch in females *Gastrotheca*
9. Skin on dorsum thick, glandular, and tuberculate; hands and feet large with large discs and extensive webbing; males having paired lateral vocal sacs behind angles of jaws (fig. 7D) and lacking projecting prepollical spines (fig. 11D) *Phrynohyas*
Skin on dorsum not thick and glandular, or, if so, hands and feet not having large discs and extensive webbing and males having single subgular vocal sacs and projecting prepollical spines; vocal sacs not behind angles of jaws 10
10. Head large, deep; arms robust; skin thick and glandular; males having projecting prepollical spines (fig. 11D) *Plectrohyla*
Males lacking projecting prepollical spines, or, if present, head shallow, arms slender, and skin not thick and glandular, or hands and feet fully webbed and dermal fringes present on arms and feet 11
11. Small frogs having pointed snouts, small or unexpanded discs, and only rudimentary webbing on hands 12
Frogs of variable size; if snouts pointed, discs expanded and hands at least one-third webbed 13
12. Dorsum rugose, discs not expanded; feet extensively webbed *Acris*
Dorsum smooth, discs barely expanded; feet slightly webbed *Pseudacris*
13. Moderate to large-sized frogs; males having paired subgular vocal sacs (fig. 7C); dorsum marked with blotches; limbs barred *Smilisca*
Size and color variable; males having single, median, subgular vocal sacs (fig. 7A) 14
14. Breeding males having large, usually brown or orange, ventrolateral glands (fig. 9A) *Ptychohyla*
Seventy-two other species *Hyla*³
- KEY TO THE SPECIES OF *Agalychnis*
1. Flanks uniformly colored, lacking vertical or diagonal bars 2
Flanks barred 6
2. Hands no more than one-half webbed; size small (males, 47 mm.; females, 62 mm.); flanks blue; dorsum usually marked with wavy transverse lines *A. saltator*
Hands at least two-thirds webbed; size larger; flanks variable; dorsum lacking wavy transverse lines 3
3. Hands immense, fully webbed, and with large discs; snout long and low 4
Hands smaller, not fully webbed, and with smaller discs; snout sloping and shorter 5
4. Hands, feet, flanks, anterior and posterior surfaces of thighs deep yellow

³ Females of *Smilisca* and *Ptychohyla*, as well as non-breeding males of the latter, will key out to *Hyla*.

- to orange; dorsum usually marked with black-bordered white spots *A. spurrelli*
- Hands, feet, flanks, anterior and posterior surfaces of thighs lacking pigment; dorsum uniform green *A. litodryas*
5. Flanks and anterior and posterior surfaces of thighs blue; iris yellow to orange in life *A. annae*
- Flanks and anterior and posterior surfaces of thighs orange; iris red in life *A. moreletii*
6. Flanks orange or yellow with dark bars; thighs and upper arms barred; dermal appendage present on heel (fig. 4B) 7
- Flanks blue or brown with creamy white bars; thighs and upper arms not barred; dermal appendage lacking on heel *A. callidryas*
7. Extensive dermal folds on forearm and large dermal flaps on foot; snout truncate *A. craspedopus*
- Only dermal appendage is flap on heel; snout sloping *A. calcarifer*
2. Dorsal surfaces of thighs unicolor 3
- Dorsal surfaces of thighs marked by dark transverse bars 4
3. Feet two-thirds webbed; large tubercles present below anal opening; shanks and feet strongly barred *H. pinorum*
- Feet fully webbed; no large tubercles below anal opening; shanks and feet weakly barred *H. nubicola*
4. Feet fully webbed *H. mixe*
- Feet three-fourths webbed 5
5. Dorsum reddish brown *H. mixomaculata*
- Dorsum yellowish tan *H. pellita*
6. Small species (males having snout-vent lengths of less than 30 mm.) with an axillary membrane (fig. 4E); dorsum usually yellow or tan; thighs uniformly yellow or tan; no difference in color on dorsal and posterior surfaces 7
- Size and axillary membrane variable; thighs not uniformly yellow or tan 16
7. Dorsolateral light stripes present; flanks usually darker than dorsum, which is unicolor yellow or tan or marked by small dark spots 8
- Dorsolateral light stripes absent; flanks variable; dorsum unicolor yellow or tan or with large markings 10
8. Head narrow; side of head and flanks dark brown; dorsolateral stripe narrow, usually extending to groin *H. robertmertensi*
- Head wider; side of head and flanks yellow; dorsolateral stripe wide, not extending to groin 9
9. Distinct dark brown flecks on forearms and shanks; small (males to 21.4 mm. in snout-vent length) *H. picta*
- No distinct dark brown flecks on forearms and shanks; larger (males to 26 mm. in snout-vent length) *H. smithii*
10. Dorsum uniform or with small flecks 11
- Dorsum with dark markings 14

KEY TO THE MIDDLE AMERICAN

SPECIES OF *Gastrotheca*

- Skin of head co-ossified with skull; no triangular dermal flap on upper eyelid; flanks and posterior surfaces of thighs darker than dorsum *G. nicefori*
- Skin of head not co-ossified with skull; a triangular dermal flap on upper eyelid (fig. 4J); flanks and posterior surfaces of thighs not darker than dorsum *G. ceratophrys*

KEY TO THE SPECIES AND SUBSPECIES OF *Hyla* IN MEXICO (NORTHWEST OF THE ISTHMUS OF TEHUANTEPEC)

1. Small species (less than 35 mm. in snout-vent length) lacking a tympanum 2
- Size variable; tympanum present (upper edge may be concealed by supra-tympanic fold) 6
10. Dorsum uniform or with small flecks 11
- Dorsum with dark markings 14

11. Dorsum uniform12
Dorsum marked by small flecks13
12. Tarsal fold present (fig. 4C); tympanic ring distinct *H. dendroscarta*
Tarsal fold absent; tympanic ring weakly defined *H. sumichrasti*
13. Diameter of tympanum less than 43 per cent of diameter of eye; large flecks on dorsum
..... *H. melanomma bivocata*
Diameter of tympanum more than 50 per cent of diameter of eye; small flecks on dorsum
..... *H. melanomma melanomma*
14. Flanks dark; dorsal pattern usually consisting of a dark hour-glass-shaped figure *H. ebraccata*
Flanks usually colored like dorsum; pattern not consisting of one large mark on back15
15. Dark chevron-shaped marks on dorsum; distinct dark bars on shanks
..... *H. sartori*
Dark dashes, sometimes interconnected to form X-shaped mark on back; ill-defined bars on shanks
..... *H. microcephala underwoodi*
16. Snout acutely rounded; digital discs small; webbing on hand vestigial; dorsum usually green with spots or dashes in a linear arrangement; a dark brown face mask present; males not exceeding 45 mm. in snout-vent length17
Snout not acutely rounded and digital discs not small, or, if so, dorsum not green and no face mask present21
17. A dark interorbital triangular mark18
No dark interorbital triangular mark19
18. Toes about two-thirds webbed; dorsum smooth *H. regilla curta*
Toes about one-half webbed; dorsum pustulate *H. regilla hypochondriaca*
19. Posterior surfaces of thighs brown with yellow spots *H. euphorbiacea*
Posterior surfaces of thighs lacking yellow spots20
20. Fifth toe webbed to base of penultimate phalanx; larger (males to 44 mm. in snout-vent length).... *H. plicata*
Fifth toe webbed to distal end of antepenultimate phalanx; smaller (males to 36 mm. in snout-vent length) *H. eximia*
21. Large frogs with a dermal fringe along the lateral edge of the forearm and foot (fig. 4A); feet nearly fully webbed; fingers two-thirds webbed... 22
Size variable; feet no more than three-fourths webbed, or, if so, fingers webbed only basally; no dermal fringe on edge of forearm and foot... 23
22. Dorsum and flanks mottled reddish brown and dark brown; prepollex in males spatulate, bare *H. valancifer*
Dorsum pale; flanks and anterior and posterior surfaces of thighs dark; prepollex in males bearing a clump of spines (fig. 11C) *H. echinata*
23. Moderate-sized frogs having round snout, pale dorsum (usually without pattern), extensive axillary membrane (fig. 4E) and fingers more than one-half webbed24
Size variable; axillary membrane absent, or, if present, pattern not as described and hands less than one-half webbed 25
24. Webbing and hidden surfaces of thighs red in life; canthus rounded; snout bluntly rounded *H. loquax*
Webbing and hidden surfaces of thighs yellow in life; canthus angular; snout acutely rounded *H. godmani*
25. Dorsum tuberculate; webbing absent on hand; dorsum dull gray or tan with irregular darker spots26
Dorsum smooth, or, if tuberculate, webbing present on hand and coloration not as described27
26. Feet about three-fourths webbed; diameter of tympanum about one-half that of eye; discs small ... *H. cadaverina*
Feet about one-half webbed; diameter of tympanum about two-thirds that of eye; discs larger *H. arenicolor*

27. Vocal slits present in males28
 Vocal slits absent in males37
28. Small frogs (snout-vent length in males less than 30 mm.); snout pointed; dorsum gray, tan, pale green, or yellow with or without dull green or brown markings29
 Larger frogs; snout not pointed, or, if so, color pattern not as described ...30
29. Head narrow; snout protruding; webbing vestigial between first and second toes (fig. 4D); nuptial excrescence absent *H. staufferi staufferi*
 Head broad, flat; snout not protruding; webbing present between first and second toes; nuptial excrescence present *H. smaragdina*
30. Dorsum uniform green or with tan mottling posteriorly; venter uniform white or yellow31
 Dorsum uniform brown or marked with dark blotches or spots; venter variable34
31. Snout acutely rounded in dorsal profile; limbs slender; anal opening at upper level of thighs; belly white ...32
 Snout bluntly rounded in dorsal profile; limbs more robust; anal opening at midlevel of thighs; belly yellow or dull cream33
32. Axillary membrane present (fig. 4E); feet two-thirds webbed; white stripe on outer edges of limbs distinct; iris red in life *H. erythromma*
 Axillary membrane absent; feet three-fourths webbed; white stripe on outer edges of limbs indistinct; iris golden in life *H. miotympanum*
33. Venter yellow; canthal stripe bronze; webbing on hands vestigial; feet one-half webbed; snout rounded in lateral profile *H. hazelae*
 Venter white to dull cream; canthal stripe black; hands one-fourth webbed; feet two-thirds webbed; snout truncate in lateral profile *H. arborescendens*
34. Snout short, truncate; venter white with black spots on chest.... *H. thorectes*
- Snout variable; venter not white with black spots on chest35
35. Transverse bands on dorsal surfaces of limbs36
 Transverse bands absent on dorsal surfaces of limbs; posterior surfaces of thighs marked with creamy yellow flecks *H. bistincta*
36. Dorsum tuberculate; diameter of tympanum less than 50 per cent that of eye; anal opening at midlevel of thighs; snout truncate in both sexes *H. chaneque*
 Dorsum smooth; diameter of tympanum more than 50 per cent that of eye; anal opening at ventral surfaces of thighs; snout acuminate and protruding in males, blunt in females *H. taeniopus*
37. Snout acuminate; fingers one-half webbed; distinct transverse bands on limbs; venter yellow; prepollex moderately enlarged and devoid of a nuptial excrescence *H. altipotens*
 Snout bluntly rounded or truncate; fingers less than one-half webbed; coloration not as described; prepollex greatly enlarged with or without nuptial excrescence38
38. Axillary membrane present (fig. 4E); nuptial excrescences absent; skin thin39
 Axillary membrane absent; nuptial excrescences present; skin thick and glandular40
39. Snout in dorsal profile truncate; diameter of tympanum less than 50 per cent of eye; feet three-fourths webbed; dorsum dark green with darker reticulations *H. charadricola*
 Snout in dorsal profile pointed; diameter of tympanum more than 50 per cent of eye; feet two-thirds webbed; dorsum yellowish tan with brown flecks *H. chryses*
40. Tympanum concealed by supratympanic fold; nuptial excrescence consisting of clump of spines (fig. 11C); snout round *H. pachyderma*

- Tympanum not concealed; nuptial ex-
crescence consisting of small spin-
ules; snout variable 41
41. Snout truncate in dorsal view; rostral
keel absent; thoracic fold absent;
dorsum pale; flanks and edges of
limbs dark brown *H. pentheter*
Snout rounded in dorsal view, or, if
truncate, a rostral keel present (fig.
4G); webbing on hand vestigial;
thoracic fold present or absent; dor-
sum not paler than flanks 42
42. Snout truncate in dorsal and lateral
profiles; rostral keel present (fig.
4G) *H. siopela*
Snout rounded in dorsal and lateral
profiles; rostral keel absent 43
43. Venter uniformly white *H. bogertae*
Venter dusky or spotted 44
44. Thoracic fold present (fig. 4F); feet
four-fifths webbed *H. robertsororum*
Thoracic fold absent; feet fully webbed
..... *H. crassa*
5. Dorsal pattern consisting of irregular
dark dashes, usually forming in X-
shaped mark in scapular region and
an interorbital bar
..... *H. microcephala underwoodi*
Dorsal pattern consisting of dark hour-
glass-shaped mark, small spots, or
nothing *H. ebraccata*
6. Snout acutely rounded; dorsum uni-
formly yellowish tan; plantar sur-
faces of feet and edge of chin suf-
fused with dark pigment
..... *H. bromeliacia*
Snout acuminate; dorsum yellow, pale
green, or pale gray with small dark
flecks or no markings; venter white 7
7. Tarsal fold absent; tympanum indis-
tinct; axillary membrane abbrevi-
ated; dorsum without dark flecks
..... *H. sumichrasti*
Tarsal fold present (fig. 4C); tym-
panum distinct; axillary membrane
extending at least midway to elbow;
dark flecks present on dorsum
..... *H. melanomma bivocata*

KEY TO THE SPECIES AND SUBSPECIES
OF *Hyla* IN NORTHERN CENTRAL AMERICA
(ISTHMUS OF TEHUANTEPEC-HONDURAS
INCLUDING YUCATAN PENINSULA)

1. Small species (less than 35 mm. in
snout-vent length) having unpig-
mented or uniformly yellow thighs;
dorsum usually yellow with darker
markings 2
Mostly larger species; thighs not uni-
formly colored or lacking pigment;
dorsum not yellow 8
2. Dorsolateral white lines present, con-
tinuous to groin or nearly so 3
Dorsolateral white lines absent, or, if
present, not extending posterior to
sacrum 4
3. Dorsolateral line broad; flanks
yellow *H. picta*
Dorsolateral line narrow; flanks and
sides of head dark brown
..... *H. robertmertensi*
4. Snout truncate in dorsal view 5
Snout acuminate or acutely rounded in
dorsal view 6
8. Moderately large species (more than
45 mm. in snout-vent length); nar-
row middorsal dark line usually pres-
ent on tan or gray dorsum; projecting
prepollex in males (fig. 11D)
..... *H. crepitans*
No middorsal dark line or projecting
prepollex 9
9. Dorsum green with or without brown
canthal stripe and brown spots or
stripes posteriorly; small species (less
than 40 mm. snout-vent length) 10
Dorsum not green, or, if so, large spe-
cies with heavy brown mottling dor-
sally and dark flanks 12
10. Dark brown canthal stripe and brown
spots or stripes usually present pos-
teriorly on dorsum 11
Dorsum uniform green or marked with
faint tan blotches or darker green
reticulations *H. miotympanum*
11. Posterior surfaces of thighs dark brown
with yellow spots *H. cuphorbiacea*
Posterior surfaces of thighs uniform
tan *H. walkeri*

12. Small species (less than 30 mm. snout-vent length) with acuminate protruding snout, dark longitudinal markings on gray or tan dorsum, and webbing reduced between first and second toes (fig. 4D) *H. staufferi staufferi*
Larger species lacking an acuminate protruding snout and having well-developed web between first and second toes; dorsal pattern variable, not linear 13
13. Dorsum tubercular; flanks dark brown or black with pale flecks; dorsum mottled black or dark brown and dark green; size large, to 80 mm. *H. chaneque*
Dorsum smooth; flanks pale; dorsum tan, pale brown, or gray, not boldly mottled; size medium, less than 50 mm. 14
14. Extensive axillary membrane (fig. 4E); webbing red in life *H. loquax*
No axillary membrane; webbing brown *H. salvadorensis*
4. Dorsum brown; toes about three-fourths webbed; skin co-ossified with skull *H. fimbriemembra*
Dorsum green; toes fully webbed; skin not co-ossified with skull *H. thysanota*
5. Dorsum green (pale tan with dark flecks in preservative); flanks and posterior surfaces of thighs unmarked; webbing red in life *H. rufitela*
Dorsum tan or brown, usually with a middorsal dark line; flanks and posterior surfaces of thighs dark or pale and marked with dark reticulations or vertical bars; webbing tan or brown in life 6
6. Fourth finger webbed to distal end of antepenultimate phalanx; snout-vent length less than 60 mm. *H. crepitans*
Fourth finger webbed to base of disc; snout-vent length of adult males more than 60 mm. 7
7. Webbing and posterior surfaces of thighs dark; calcar present (fig. 4B); palpebral membrane reticulated (fig. 5A); hands huge *H. boans*
Webbing pale; posterior surfaces of thighs marked by narrow vertical bars; calcar absent; palpebral membrane clear; hands smaller *H. rosenbergi*
8. Snout protruding beyond lower jaw (fig. 3E); webbing vestigial between first and second toes (fig. 4D) 9
Snout not protruding beyond lower jaw; webbing not reduced between first and second toes 14
9. Larger frogs (males to 50 mm. snout-vent length); thighs strongly barred; supratympanic fold black; dorsum blotched or spotted 10
Smaller frogs (males to 40 mm. snout-vent length); thighs weakly barred or plain; supratympanic fold pale brown; dorsum having linear pattern 11
10. Dorsum tuberculate; snout subacuminate; vocal sac flecked with brown;

KEY TO THE SPECIES AND SUBSPECIES
OF *Hyla* IN LOWER CENTRAL AMERICA
(NICARAGUA-PANAMA)

1. Larger species (adult males more than 40 mm. in snout-vent length); feet at least three-fourths webbed; a projecting prepollex present 2
Smaller species (adult males less than 50 mm. in snout-vent length); webbing of feet variable; prepollex enlarged or not, but never projecting 8
2. A scalloped dermal fringe along outer edge of forearm and fourth finger and along outer edge of foot and fifth toe (fig. 4A) 3
No scalloped dermal fold on outer edges of limbs 5
3. Dorsum tubercular; general dorsal coloration brown; hands and feet immense; osteoderms present in adults *H. miliaria*
Dorsum smooth or nearly so 4

- tarsal fold weak; fingers lacking web; black spots absent in scapular region *H. Boulengeri*
- Dorsum smooth; snout pointed; vocal sac dark gray; tarsal fold absent; trace of web between fingers; two or more elongate black spots in scapular region *H. rostrata*
11. Snout-vent length more than 30 mm.; diameter of tympanum at least two-thirds of the diameter of the eye; prevomerine elevations about the size of the choanae12
- Snout-vent length less than 30 mm.; tympanum less than half of the diameter of the eye; prevomerine elevations smaller than choanae13
12. Thighs mottled posteriorly; discs on fingers about half of the diameter of the tympanum; canthal line faint
..... *H. rubra*
- Thighs faintly barred or plain posteriorly; discs on fingers about size of tympanum; canthal line distinct....
..... *H. elaeochroa*
13. Dorsum brown with irregular dorso-lateral stripes and interrupted paravertebral stripes; two transverse bars on shanks; interorbital bar present *H. stauferi stauferi*
- Dorsum gray with complete dorsolateral and paravertebral stripes; longitudinal stripe on shank; interorbital bar absent *H. stauferi altae*
14. Small (males to 30 mm.) yellow frogs with brown dorsal markings and uniformly yellow thighs15
- Size variable (mostly larger than 30 mm.); thighs not uniformly yellow18
15. Head broad; scalloped dark mark on dorsal surface of shank; dorsum plain or marked by brown spots or hour-glass-shaped mark.... *H. ebraccata*
- Head narrow; narrow transverse dashes or longitudinal dark line on shank; dorsum marked with narrow brown dashes, longitudinal lines, or reticulations16
16. Lateral dark stripe, bordered above by narrow white line, extending from snout at least to sacral region17
- Lateral dark stripe indistinct, present only above tympanum and insertion of arm; dorsal markings consisting of narrow lines and dashes, sometimes interconnected *H. phlebodes*
17. Lateral dark stripe continuous to groin; dorsal pattern consisting of a pair of narrow dark longitudinal lines; dashes or longitudinal line on shanks; interorbital dark bar absent
..... *H. microcephala microcephala*
- Lateral dark stripe extending to sacral region; dorsal pattern consisting of interconnecting lines and dashes; transverse bars on shanks; interorbital dark bar present
..... *H. microcephala underwoodi*
18. Dorsum uniformly yellow or tan, or with small dark brown or red flecks; venter immaculate; granules above insertion of arm; temporal region enlarged19
- Dorsum not uniformly yellow or tan, or, if so, venter spotted; no granules above insertion of arm; temporal region not enlarged20
19. Two denticles at symphysis of lower jaw; dark flecks on lips, side of head and temporal region; size larger (males to 32.8 mm.) *H. picadoi*
- One denticle at symphysis of lower jaw; dark flecks present on lips in some; size smaller (males to 23.5 mm.) *H. zeteki*
20. Webbing and posterior surfaces of thighs red21
- Webbing and posterior surfaces of thighs not red22
21. Snout long; dorsum tan with brown blotches, flanks spotted; nuptial excrescence extensive in breeding males *H. pseudopuma infucata*
- Snout short; dorsum uniform tan, gray, or brown; flanks cream, unmarked; nuptial excrescences absent....*H. loquax*

22. Dorsum tan with narrow cream dorso-lateral stripes; flanks dark brown; venter flecked with black *H. angustilineata*
Dorsum not marked with cream dorso-lateral stripes 23
23. Iris red in life (usually red or reddish brown in preservative); a white lateral stripe present; no yellow spots on flanks or thighs; dorsum green or dark brown 24
Iris not red in life or preservative; no white lateral stripe; yellow spots present or not on flanks and thighs; dorsum tan or green, blotched, streaked, mottled, or unicolor 26
24. Fingers one-half webbed; vocal sac in breeding males dark gray ... *H. legleri*
Fingers one-fourth webbed; vocal sac in breeding males white or creamy yellow 25
25. White labial stripe usually expanded below eye; dorsum dark green or brown; plantar surfaces of feet pigmented; diameter of tympanum less than 50 per cent of diameter of eye....
..... *H. rufioculis*
White labial stripe not expanded below eye; dorsum green; plantar surfaces of feet unpigmented; diameter of tympanum more than 50 per cent of diameter of eye *H. uranochroa*
26. Posterior surfaces of thighs unpigmented except for a yellow spot bordered by black; narrow vertical white rostral line continuous with white line on canthus, edge of eyelid, and supratympanic fold; two vertical white or yellow bars on upper lip; size small (26 mm.) ... *H. subocularis*
Color not as described 27
27. Dorsum tan, yellow, or pale gray with dark brown streaks, spots, or blotches 28
Dorsum green or brown, spotted, mottled, or plain; if tan, no markings evident 29
28. Snout acuminate; dorsum usually tan or yellow with large brown spots or blotches; posterior surfaces of thighs dark brown; flanks brown with yellow spots; venter immaculate; size medium (48 mm.)
..... *H. pseudopuma pseudopuma*
Snout truncate; dorsum pale tan, yellowish tan, or pale gray with brown or gray streaks; posterior surfaces of thighs pale brown; flanks cream; venter spotted or flecked with black; size small (36 mm.) *H. rivularis*
29. Dorsum pale green or tan (nearly white with scattered dark pigment in some specimens); white stripe on canthus, edge of eyelid, and supratympanic fold; large mental gland usually evident *H. colymba*
Color not as described; not mental gland present 30
30. Posterior surfaces of thighs yellow or white with black spots or vertical bars; flanks black and white; snout very short, truncate; fleshy spines present in some populations
..... *H. lancasteri*
Posterior surfaces of thighs dark, unicolor, or with small pale spots; snout not especially short; flanks not boldly marked with black and white 31
31. Dorsum uniform green or with small dark flecks; broad tan canthal stripe present 32
Dorsum mottled green, black, and brown (uniform green in some females); no canthal stripe 33
32. Continuous white labial stripe; flanks and thighs dark brown with yellow spots *H. xanthosticta*
Labial stripe interrupted, expanded below eye; posterior surfaces of thighs yellow; flanks white *H. debilis*
33. Snout angular in lateral profile; diameter of tympanum equal to about one-third of diameter of eye
..... *H. pictipes*
Snout rounded in lateral profile; diameter of tympanum equal to about one-half of diameter of eye ... *H. tica*

KEY TO THE MIDDLE AMERICAN SPECIES
OF *Phyllomedusa*

- Small frog (male, 40 mm.); first toe shorter than, and not opposable to second; parotoid glands absent; venter uniform creamy yellow *P. lemur*
- Large frog (female, 86 mm.); first toe longer than and opposable to second; parotoid glands forming elevated dorsolateral ridge; venter orange and dark brown with white spots on chest *P. venusta*

KEY TO THE SPECIES OF *Plectrohyla*

1. Prepollical process bifid 2
Prepollical process flat, spur-like, or truncate, but not bifid 3
2. Flanks and anterior surfaces of thighs pale with bold vertical dark bars
..... *P. hartwegi*
Flanks and anterior surfaces of thighs not marked with contrasting colors
..... *P. guatemalensis*
3. Prepollical process flat, not protruding; vocal slits absent 4
Prepollical process round or pointed; vocal slits present or absent 5
4. Dorsum tubercular; snout bluntly rounded *P. pycnochila*
Dorsum smooth or with few scattered tubercles; snout acuminate
..... *P. glandulosa*
5. Prepollical process elongate, round, terminally blunt; vocal slits absent
..... *P. lacertosa*
Prepollical process knife-like, terminally pointed; vocal slits present or absent 6
6. Large species (90 mm.); vocal slits absent; dorsum smooth except for tubercles on head *P. avia*
Small species (less than 50 mm.); vocal slits present; dorsum tubercular or smooth (if smooth, no tubercles on head) 7
7. Vertical rostral keel present (fig. 4G and H) 8
Vertical rostral keel absent 9

8. Snout acuminate; dorsum smooth or weakly tuberculate; small dark flecks on flanks *P. sagorum*
Snout blunt; dorsum tuberculate; large brown spots on flanks *P. quecchi*
9. Snout acuminate; dorsum smooth or weakly tuberculate; lateral light stripe bordered below by narrow dark line usually present *P. ixil*
Snout truncate; dorsum tuberculate; lateral dark line usually present, but light stripe absent *P. matudai*

KEY TO THE SPECIES OF *Pternohyla*

- Bony ridge extending from point between nostrils to tip of snout; snout in dorsal profile acutely rounded; tips of digits expanded into small discs; outer edge of inner metatarsal tubercle elevated (fig. 4C); vocal sacs connected medially in breeding males *P. fodiens*
- No bony ridge extending anteriorly from a point between nostrils; snout bluntly rounded in dorsal profile; tips of digits not expanded; inner metatarsal tubercle round in section; vocal sacs widely separated medially in breeding males *P. dentata*

KEY TO THE SPECIES AND SUBSPECIES
OF *Ptychohyla*

1. A weak tarsal fold; outer fingers one-third webbed; males having nuptial spines (fig. 11C); color in life tan or brown with blotches or reticulations, never green; iris bronze or copper 2
No tarsal fold; outer fingers having only vestige of web; males lacking nuptial tuberosities; color in life green or brown, iris red or bronze 5
2. Chest, throat, and flanks usually having black or brown spots; no distinct white stripe on upper lip or on flanks; a faint white line usually present above anus; a rostral keel present 3
Chest, throat, and flanks usually unspotted; distinct white line on upper

- lip and on flank present or not; white line above anus faint or well defined; no rostral keel 4
3. Interorbital distance much greater than width of eyelid; spots on throat and chest black; spots only occasionally present on belly; flanks marbled with black and white; nuptial spines small, as many as 80 on one thumb.....
..... *P. leonhardschultzei*
- Interorbital distance about equal to width of eyelid; spots on chest and throat brown or black; spots usually present on belly; flanks having round brown or black spots; nuptial spines moderate in size, conical, seldom more than 60 on one thumb
..... *P. spinipollex*
4. A distinct, broad, white lateral stripe usually present; usually a distinct white line above anus; a distinct white stripe on upper lip
..... *P. euthysanota euthysanota*
- No white lateral stripe; a faint white stripe above anus; no distinct white stripe on upper lip
..... *P. euthysanota macrotypanum*
5. A distinct, broad, lateral stripe; a white stripe on upper lip expanded to form a large spot below eye; hidden surfaces of thighs and webs of feet not orange to red in life; internarial area slightly depressed; diameter of tympanum greater than one-half diameter of eye 6
- No lateral white stripe; no stripe on upper lip; in life dorsum green; hidden surfaces of thighs and webs of feet orange or red; internarial area flat; diameter of tympanum less than one-half diameter of eye *P. ignicolor*
6. Webs of feet and posterior surfaces of thighs cream; dorsum in life reddish brown; iris bright red
..... *P. schmidtorum schmidtorum*
- Webs of feet and posterior surfaces of thighs pale brown; dorsum in life green; iris reddish bronze
..... *P. schmidtorum chamulae*

KEY TO THE SPECIES OF *Smilisca*

1. Larger frogs (males, 76 mm.; females, 90 mm.) having broad, flat heads and a dark brown or black postorbital mark encompassing tympanum 2
- Smaller frogs (males, 45 mm.; females, 84 mm.) having narrower heads and lacking a dark brown or black postorbital mark encompassing tympanum 4
2. Lips barred; flanks cream with bold brown or black mottling in groin; posterior surfaces of thighs brown with cream flecks *S. baudinii*
- Lips not barred; narrow white labial stripe present; flanks not cream with bold brown or black mottling in groin; posterior surfaces of thighs variable 3
3. Flanks and anterior and posterior surfaces of thighs dark brown with pale blue spots on flanks and blue spots on thighs *S. cyanosticta*
- Flanks cream with fine black venation; posterior surfaces of thighs pale brown with or without darker flecks of small cream spots *S. phaeota*
4. Fingers having only vestige of web; diameter of tympanum two-thirds that of eye; dorsum tan with pair of broad brown stripes *S. puma*
- Fingers about one-half webbed; diameter of tympanum about one-half that of eye; dorsum variously marked with spots or blotches 5
5. Snout short, truncate; vocal sacs in breeding males dark gray or brown; blue spots on flanks and posterior surfaces of thighs *S. sila*
- Snout long, sloping, rounded; vocal sacs in breeding males white; cream or pale blue flecks on flanks and posterior surfaces of thighs *S. sordida*

KEY TO SPECIES AND SUBSPECIES
OF *Tripidon*

1. Tip of snout upturned; dermal sphen-

- ethmoid visible through skin; odontoids absent from palatines; vocal sac bilobate *T. petasatus*
- Tip of snout not upturned; dermal sphenethmoid absent; odontoids present on palatines; vocal sac single and median 2
2. Dorsum uniformly yellowish-tan to olive-green or marked by minute flecks or dashes
 *T. spatulatus spatulatus*
- Dorsum yellowish tan with dark brown reticulations and spots
 *T. spatulatus reticulatus*

ACCOUNTS OF THE GENERA AND SPECIES

Genus *Pachymedusa* Duellman

Pachymedusa Duellman, 1968b, p. 5 [type species, *Phyllomedusa dacnicolor* Cope, 1864, by original designation].

GENEROTYPE: *Phyllomedusa dacnicolor* Cope, 1864, by original designation (Duellman, 1968b). Cope (1866b) placed *dacnicolor* in the genus *Agalychnis* Cope, 1865a, and the species has since led a spotted history of transfer between *Agalychnis* and *Phyllomedusa*.

ETYMOLOGY: The generic name is derived from the Greek *pachy*, meaning thick, and the Greek *Medousa* (Latin *Medusa*), used in reference to *Phyllomedusa* and alluding to the heavy body of *Pachymedusa dacnicolor*.

DEFINITION: Frogs of the genus *Pachymedusa* are large and have a green dorsum and white spots on the flanks. The pupil is vertically elliptical, and the iris is golden yellow with black reticulations; the palpebral membrane is reticulated. The fingers and toes are webbed basally and have narrow lateral fringes; the terminal discs are large. The first toe is shorter than the second and not opposable to the others. The skin on the dorsum is smooth or shagreened and lacks osteoderms; the paratoid glands are diffuse. There is no integumentary-cranial co-ossification. The vocal sac is single, median, and subgular. The tongue is much longer than wide and attached only anteriorly. Breeding males have horny brown nuptial excrescences on the thumbs. The skull is deep; its depth is more than half of its length (fig. 21). The parietal plane is barely inclined anteroventrally. The skull is characterized by a large frontoparietal fontanelle, robust quadratojugals, and moderately developed squamosals with long posterior arms and short anterior arms that extend only about one-fourth of the distance to the maxillaries. The premaxillary has a well-developed, posterodorsally inclined alary process. The maxillary bears a moderately deep pars facialis, which at the level of the palatine extends dorsally and connects with the short maxillary process of the nasal. The nasals are large, narrowly separated medially, and in bony contact with the sphenethmoid. The canthal ridge is parallel to the maxillary.

The maxillary process of the nasal articulates with the posterior process of the pars facialis. The sphenethmoid is well ossified. The dentigerous processes of the prevomers are short and situated at an angle to the midline. The pterygoids are robust and have a cartilaginous attachment to the prootics. The otic region is moderately small. Teeth are present on the premaxillaries, maxillaries, and prevomers, but absent from the palatines and parasphenoid. The teeth are barely spatulate and strongly bifid. The tadpoles are pelagic types with anterior mouths. The lips are infolded laterally and bordered by small papillae, except that the median part of the upper lip is bare. There are two upper and three lower rows of teeth. The spiracle is ventral on the body and sinistral to the midline. The caudal musculature is slender, and the fins are deep. The mating call is a single, short, poorly modulated note. The haploid number of chromosomes is 13.

COMPOSITION OF GENUS: One species, *P. dacnicolor*, is included in the genus. Eight hundred and forty-seven preserved frogs, seven skeletons, five lots of tadpoles, and three preserved clutches of eggs have been examined.

DISTRIBUTION: *Pachymedusa* occurs on the Pacific slopes and lowlands from southern Sonora to the Isthmus of Tehuantepec, México.

DISCUSSION: Duellman (1968b) suggested that *Pachymedusa* is a generalized and probably primitive phyllomedusine and represents a hanging relict in the Mesoamerican herpetofauna. In this respect, the genus is like *Hylacophryne* in the Leptodactylidae (Lynch, 1968).

Pachymedusa dacnicolor (Cope)

Phyllomedusa dacnicolor Cope, 1864, p. 181 [holotype, formerly in U.S.N.M., now lost, from "near Colima," México; John Xantus collector; type locality restricted to Colima, Colima, México by Smith and Taylor (1950, p. 328)]. Brocchi, 1882, p. 68. Boulenger, 1882a, p. 426. Kellogg, 1932, p. 143. Funkhouser, 1957, p. 37.

Agalychnis dacnicolor Cope, 1866b, p. 86 [transfer of *Phyllomedusa dacnicolor* Cope to *Agalychnis* Cope, 1865a]. Günther, 1901 (1885-1902), p. 291.

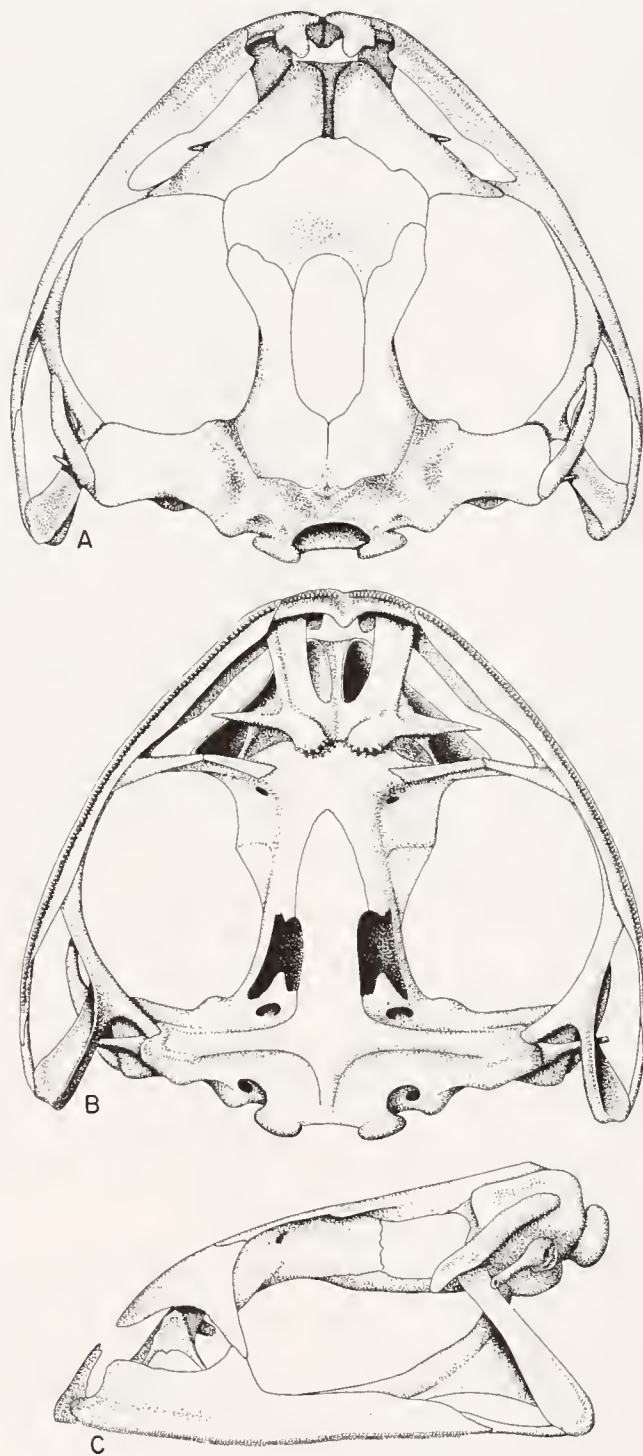


FIG. 21. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Pachymedusa dacnicolor*, K.U. No. 84916. $\times 3$.

Smith and Taylor, 1948, p. 72. Duellman, 1957, p. 29 [synonymized *Agalychnis alcorni* Taylor, 1952b, with *Agalychnis dacnicolor* (Cope, 1864)].

Agalychnis alcorni Taylor, 1952b:31, pl. 1 [holotype, K.U. No. 29763 from "south bank Río de Tepalcatepec, 800 feet elevation, 17 miles south of Apatzingán, Michoacán," México; J. R. Alcorn collector.

Phyllomedusa alcorni: Funkhouser, 1957, p. 30 [transfer of *Agalychnis alcorni* Taylor, 1952b, to *Phyllomedusa* Wagler, 1830].

Pachymedusa dacnicolor: Duellman, 1968b, p. 5 [designation of *Phyllomedusa dacnicolor* Cope as type species of *Pachymedusa*].

DIAGNOSIS: This large species differs from other phyllomedusine frogs in having relatively long and slender fingers and toes with little webbing, short legs, a high head, a gold and black eye; white spots or bars on otherwise uniformly green flanks, and cream-colored thighs. The hand is about one-fourth webbed, and the foot is about one-third webbed. The only *Agalychnis* lacking blue, yellow, or orange on the flanks and thighs is *litodryas*, which has fully webbed hands and feet, a shallow head, a dark red eye, and unpigmented flanks and thighs. The Middle American species of *Phyllomedusa* lack webbing.

DESCRIPTION: Males of this large species attain a maximum snout-vent length of 82.6 mm., and females reach 103.6 mm. In a series of 20 males from Villa Unión, Sinaloa, México, the snout-vent length is 63.1 to 73.1 (mean, 67.6) mm.; the ratio of tibia length to snout-vent length is 0.341 to 0.415 (mean, 0.372); the ratio of foot length to snout-vent length is 0.289 to 0.362 (mean, 0.332); the ratio of

head length to snout-vent length is 0.296 to 0.322 (mean, 0.313); the ratio of head width to snout-vent length is 0.292 to 0.345 (mean, 0.316), and the ratio of the diameter of the tympanum to that of the eye is 0.587 to 0.754 (mean, 0.690). Three females from the same locality have snout-vent lengths of 72.0 to 87.6 (mean, 79.2) mm. The females show no significant differences in proportions from the males. Some geographic variation in sizes and proportions is evident (table 6). Individuals of both sexes are noticeably larger in the southern part of the range. The snout-vent length in 20 specimens from the vicinity of Pochutla, Oaxaca, varies from 71.8 to 82.6 (mean, 77.5) mm. Individuals from the Balsas Basin in Morelos have proportionately larger tympani; the average ratio of the diameter of the tympanum to that of the eye is 0.735; whereas the highest ratio in coastal samples is 0.690.

The head is noticeably narrower than the body, and the top of the head is flat. In dorsal profile the snout is rather acutely rounded. In lateral profile, in males, the snout is gently sloped from the eyes to the nostrils and then inclined gradually to the tip of the snout; in females, the snout is inclined gently from the eyes to a point just anterior to the nostrils and then steeply inclined to the tip of the snout (fig. 22). The snout is moderately short, and the nostrils are barely protuberant and situated at a point about two-thirds of the distance from the eyes to the tip of the snout in females and about midway between the eyes and the tip of the

TABLE 6
Geographical Variation, with Means in Parentheses, in Males of *Pachymedusa dacnicolor*.

Locality	N	Snout-vent Length (mm.)	Tibia Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
Sinaloa: Villa Unión	20	63.1-73.1 (67.6)	0.341-0.415 (0.372)	0.292-0.345 (0.316)	0.587-0.754 (0.690)
Jalisco: Melaque-La Resolana	7	58.1-71.9 (65.1)	0.399-0.433 (0.420)	0.323-0.341 (0.329)	0.591-0.727 (0.638)
Michoacán: Coalcomán	20	62.2-75.6 (68.8)	0.391-0.439 (0.416)	0.318-0.337 (0.324)	0.587-0.742 (0.651)
Morelos: Cuautlixco	12	64.5-74.0 (70.2)	0.351-0.411 (0.379)	0.306-0.363 (0.333)	0.639-0.804 (0.735)
Oaxaca: Pochutla	20	71.8-82.6 (77.5)	0.388-0.446 (0.407)	0.301-0.335 (0.317)	0.575-0.781 (0.665)

snout in males. The canthus is rounded; the loreal region is barely concave, and the lips are thick and moderately flared. A thin dermal fold extends posteriorly from the eye above the tympanum, and around the posterior edge of the tympanum and downward in a distinct fold to the point of insertion of the arm. The fold obliterates the upper edge of the tympanum in all individuals and the posterior edge of the tympanum in about half

of the specimens. Otherwise, the tympanum is distinct and separated from the eye by a distance equal to about one-third to one-half of the diameter of the tympanum.

The upper arms are slender, and the forearms are robust. A few small tubercles are present on the ventral surface of each forearm, and a distinct, thin, transverse dermal fold is present on the wrist. The fingers are short, robust, and bear moderately large discs; the diameter of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The subarticular tubercles are large, subconical, and present on the proximal segments of each digit. A large, flattened, tripartite palmar tubercle is present. An elongate, elevated tubercle is present on the prepollex, which is moderately enlarged and in breeding males bears a horny nuptial excrescence. Webbing is absent between the first and second fingers and rudimentary between the others (fig. 23A). The hind limbs are very short and robust; the heels of the adpressed limbs barely meet. The tibiotarsal articulation extends to the axilla. A thin, transverse dermal fold is present on the heel, and a distinct, elevated tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small and conical. The toes are short and heavy and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately large and round; the supernumerary tubercles are large and conical. The toes are no more than one-third webbed (fig. 23B). A narrow dermal fringe is present along the edge of the toe.

The anal opening is directed ventrally at the midlevel of the thighs. A long, broad anal sheath is present; laterally the anal sheath extends to the ventral surfaces of the thighs. The skin on the dorsum is smooth or shagreened; in some individuals minute pustules are present above the insertion of the arm. The throat, belly, and ventral surfaces of the thighs are heavily granular. Weak granules are evident on the ventral surfaces of the forearms in some specimens; the ventral surfaces of the shanks, feet, and upper arms are smooth. Distinct, elevated pustules are present on the flanks in most specimens. The tongue is elongate, about twice as long as

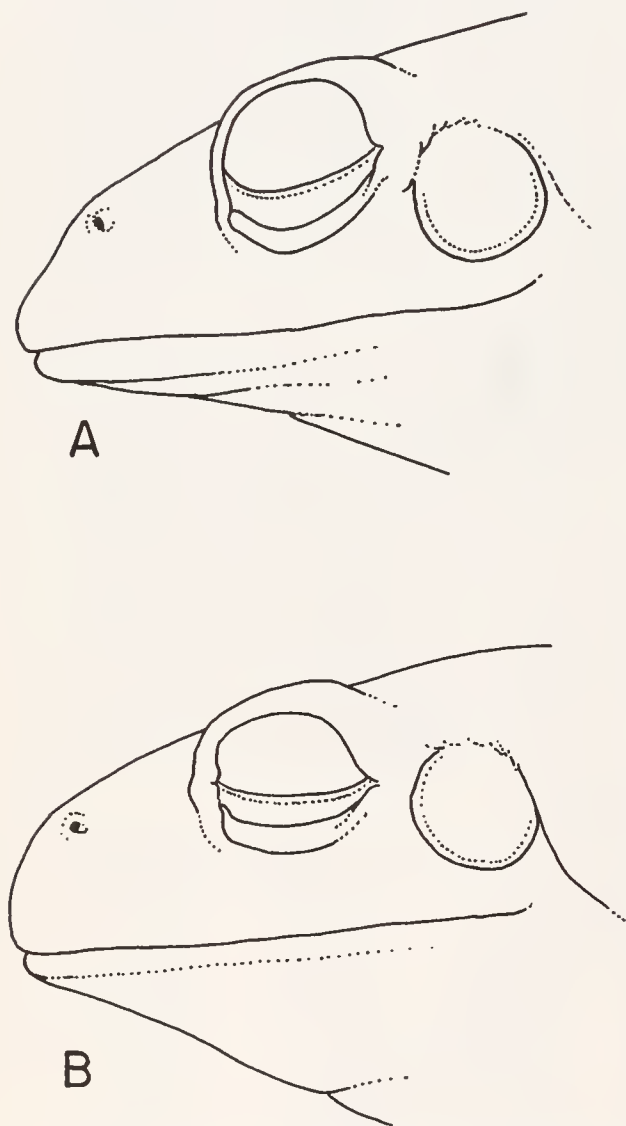


FIG. 22. Lateral views of heads of *Pachymedusa dacnicolor* showing sexual dimorphism in the shape of the snout. A. Male, K.U. No. 78442. B. Female, K.U. No. 78435. $\times 2$.

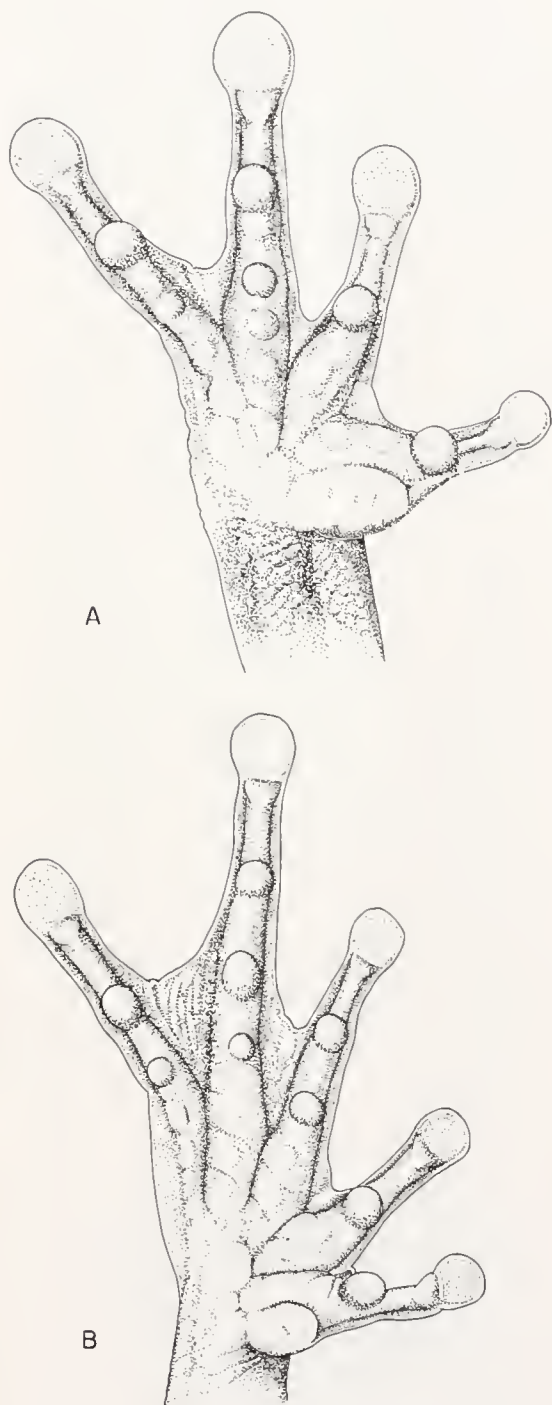


FIG. 23. Hand (A) and foot (B) of *Pachymedusa dacnicolor*, K.U. No. 87138. $\times 3$.

wide. In some individuals it is deeply notched posteriorly, whereas in others it is shallowly notched or entire; posteriorly, the tongue is free for about one-third of its length. The dentigerous processes of the prevomers are small oblique elevations situated between the moderately large, nearly quadrangular choanae. In the series of males from Villa Unión, Sinaloa, individuals have three to six teeth on each process and males have a total of six to 11 (mean, 8.8) prevomerine teeth. Females in the same series have five or six teeth on each process and a total of 10 to 12 (mean, 11.0) prevomerine teeth. The vocal slits extend along the inner edge of the posterior part of the lower jaw. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Pachymedusa dacnicolor* is green above and dirty white below (pl. 41, fig. 1). The dorsum usually is a rather bright green. Individuals are capable of changing the intensity of the color so that the color change in one individual can range from a pale leaf-green to a dark dull green. The throat and belly are dirty white or creamy white, and the ventral surfaces of the hind limbs vary from pinkish orange to orangetan. Pale creamy white flecks, spots, or vertical bars are present on the flanks, and in some specimens creamy white or yellow flecks, narrowly outlined with black in some specimens, are present on the dorsum. The iris is a dark golden bronze heavily flecked with black.

Individuals from the northern part of the range, Colima northward, have few, if any, creamy white or yellow spots on the dorsum, whereas individuals from Michoacán and Morelos usually have a few distinct dorsal spots. Specimens from Guerrero and especially Oaxaca have many white or pale yellow spots on the dorsum. Individuals from the northern part of the range have small creamy white flecks on the flanks. In specimens from Colima and Michoacán the amount of white is increased on the flanks and tends to fuse into short, vertical bars and irregular spots. Individuals from the southern part of the range, Guerrero and Oaxaca, have much more white on the flanks; usually the flanks are marked by short, vertical white bars.

In preservative, the dorsum is dull blue

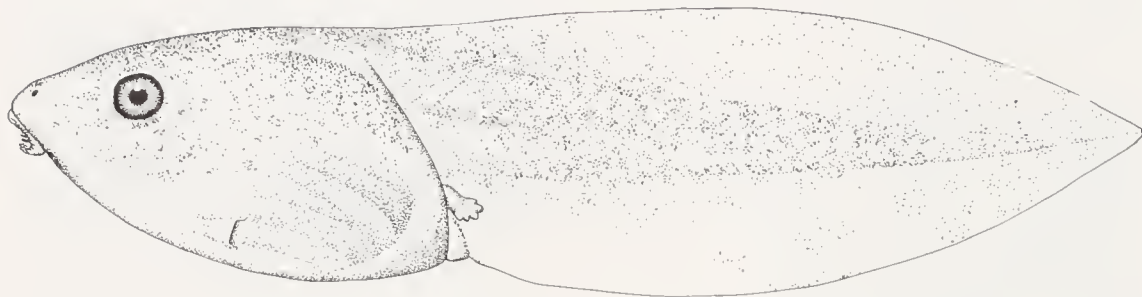


FIG. 24. Tadpole of *Pachymedusa dacnicolor*, L.A.C.M. No. 1808. $\times 3$.

or bluish gray; the venter is creamy white. The markings on the flanks and spots on the dorsum are dull creamy white.

TADPOLES: A typical tadpole in developmental stage 34 has a body length of 17.2 mm. and a total length of 45.1 mm. The body is noticeably deeper than wide; it is deepest at a point about three-fourths of the length of the body. In dorsal profile the snout is truncate; in lateral profile it is acutely rounded. The nostrils are small, dorsolateral, directed anterolaterally, and situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The eyes are relatively small and directed dorsolaterally. The spiracle is ventral and sinistral to the midline; the spiracular opening is at a point about midway between the snout and the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is moderately deep and gradually diminishes to a thin distal portion. The dorsal fin does not extend onto the body and is deepest at midlength of the tail; the ventral fin has an equal depth throughout the anterior half of the tail. Posteriorly both fins are considerably narrower. The depth of the caudal musculature at midlength of the tail is about equal to the depth of each of the fins (fig. 24).

In life the tadpoles are bluish gray, except for the fins which are nearly transparent. In preservative, they are pale creamy tan with minute clusters of pigment on the dorsal surfaces of the body and on the caudal musculature; minute flecks are present on the fins.

The mouth is moderately small, antero-ventral in position and directed anteriorly. Moderately deep lateral folds are present in

the lips, which are bordered by a single row of papillae, except for the median third of the upper lip which is bare. Many papillae are present in the lateral fold. The beaks are moderately heavy and bear distinct serrations. The upper beak forms a broad arch with long, slender lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are long and extend laterally nearly to the papillae; the second upper row is interrupted medially. The lower rows are progressively shorter than the upper ones. In most individuals, the lower rows are complete, but in some the first lower tooth row is narrowly interrupted medially (fig. 25).

MATING CALL: The call of *Pachymedusa dacnicolor* consists of a single note, resembling "cluck." The notes are repeated at intervals of a few seconds to several minutes. Each note has a duration of 0.16 to 0.36 (mean, 0.23) of a second and has a pulse rate of 120 to 190 (mean, 159) pulses per second. The fundamental frequency varies from 116 to 171 (mean, 153) cycles per second, and the

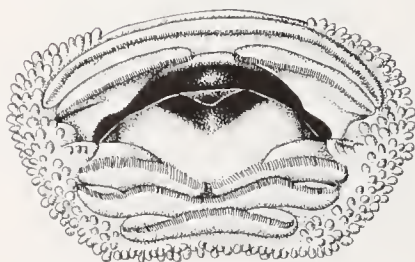


FIG. 25. Mouth of tadpole of *Pachymedusa dacnicolor*, L.A.C.M. No. 1808. $\times 12$.

dominant frequency varies from 1120 to 2240 (mean, 1727) cycles per second (pl. 37, fig. 2).

NATURAL HISTORY: *Pachymedusa dacnicolor* inhabits xeric tropical lowlands characterized by a prolonged dry season. In this habitat of western México, *P. dacnicolor* is one of the few amphibians that is active in the dry season. I have observed individuals perched on the branches of scrubby trees in the Balsas Basin in March and April. Hardy and McDiarmid (1968) noted that individuals of this species were observed on roads in Sinaloa in the dry season. In the rainy season (June through October) males call from large herbs, bushes, or trees around temporary pools. Claspings pairs have been observed in trees and bushes. Usually the eggs are deposited on leaves overhanging the water, but Taylor (1942a, p. 40) noted that on occasion the eggs are deposited on the ground a few inches above the water in pools where no trees or plants are present. Zweifel and Norris (1955, p. 233) reported a mass of eggs on a grassy bank above the water in a small stream in Sonora. Duellman (1961e, p. 44) noted 100 to 350 eggs in each of 15 clutches at Coaleomán, Michoacán. The eggs are pale green and are located only in the exterior part of the clear gelatinous mass. Two composite egg masses were apparently made up of egg deposition on the part of three to five females.

The tadpoles develop in shallow ponds where they swim freely, but take refuge amidst aquatic vegetation. In open water, the tadpoles orient with their heads up and the bodies forming an angle of about 45° with the surface of the water.

REMARKS: Sexual dimorphism in the shape of the snout is common among phyllomedusine frogs. Taylor (1952b) named *Agalychnis alcorni* and used the sexually dimorphic shape of the snout as the principle diagnostic character of his new species. Funkhouser (1957) apparently was unaware of the significance of the shape of the snout and placed *alcornii* in a separate phyletic line from *dacnicolor*. Duellman (1957) demonstrated the sexual dimorphism in the shape of the snout in *dacnicolor* and placed *alcornii* in the synonymy of *dacnicolor*.

ETYMOLOGY: The specific name *dacnicolor*

apparently is derived from the Greek *dacno*, meaning bite or sting, and the Latin *color*; the meaning implied by Cope is not understood.

DISTRIBUTION: *Pachymedusa dacnicolor* inhabits xeric lowlands and lower montane slopes to elevations of about 1000 meters from southern Sonora to the Isthmus of Tehuantepec, México, including the Balsas Basin (fig. 26).

See Appendix 1 for the locality records of the 862 specimens examined.

Genus *Agalychnis* Cope

Agalychnis Cope, 1864, p. 181 [no species designated]; 1865a, p. 110 [*H. moreletii*, *holochlora*, and *callidryas* listed]. Taylor, 1952c, p. 801 [designation of *Hyla moreletii* Duméril as the generotype].

GENEROTYPE: *Hyla moreletii* Duméril, 1853, by subsequent designation (Taylor, 1952c). Most authorities, such as Smith and Taylor (1948), Funkhouser (1957), and Goin (1961b), gave *Hyla callidryas* Cope, 1862, as the generotype and the date of the genus as 1864. Cope (1864, p. 181) in his discussion of his new species, *Phyllomedusa dacnicolor*, stated in reference to *dacnicolor*: "It affords an easy passage to the true Hylae, whose family it enters, by the genus *Agalychnis* Cope, and *H. moreletii* and *holochlora* are the other species." It was not until the following year that Cope (1865a, p. 110) associated his *Hyla callidryas* with the genus *Agalychnis*; a footnote to *Agalychnis* in his key to the genera of hylids contained the following statement: "Embraces *Hyla moreletii*, Dum., *H. holochlora*, Salvin, and *H. callidryas*, Cope."

The determination of the availability of the generic name dating from 1864 rests on the interpretation of Cope's statement, "and *H. moreletii* and *holochlora* are the other species." It almost seems as though he forgot *callidryas*. However, his statement in the footnote (1865a, p. 110) clearly listed the species that he included in the genus. Because *Hyla moreletii* is the first species listed in 1865, as well as in the noncommittal statement given in 1864, and because no specific designation of the generotype was made by Cope in either paper or in his subsequent writings, *Hyla moreletii* Duméril, 1853, is the correct generotype, Cope (1864, p. 181) did

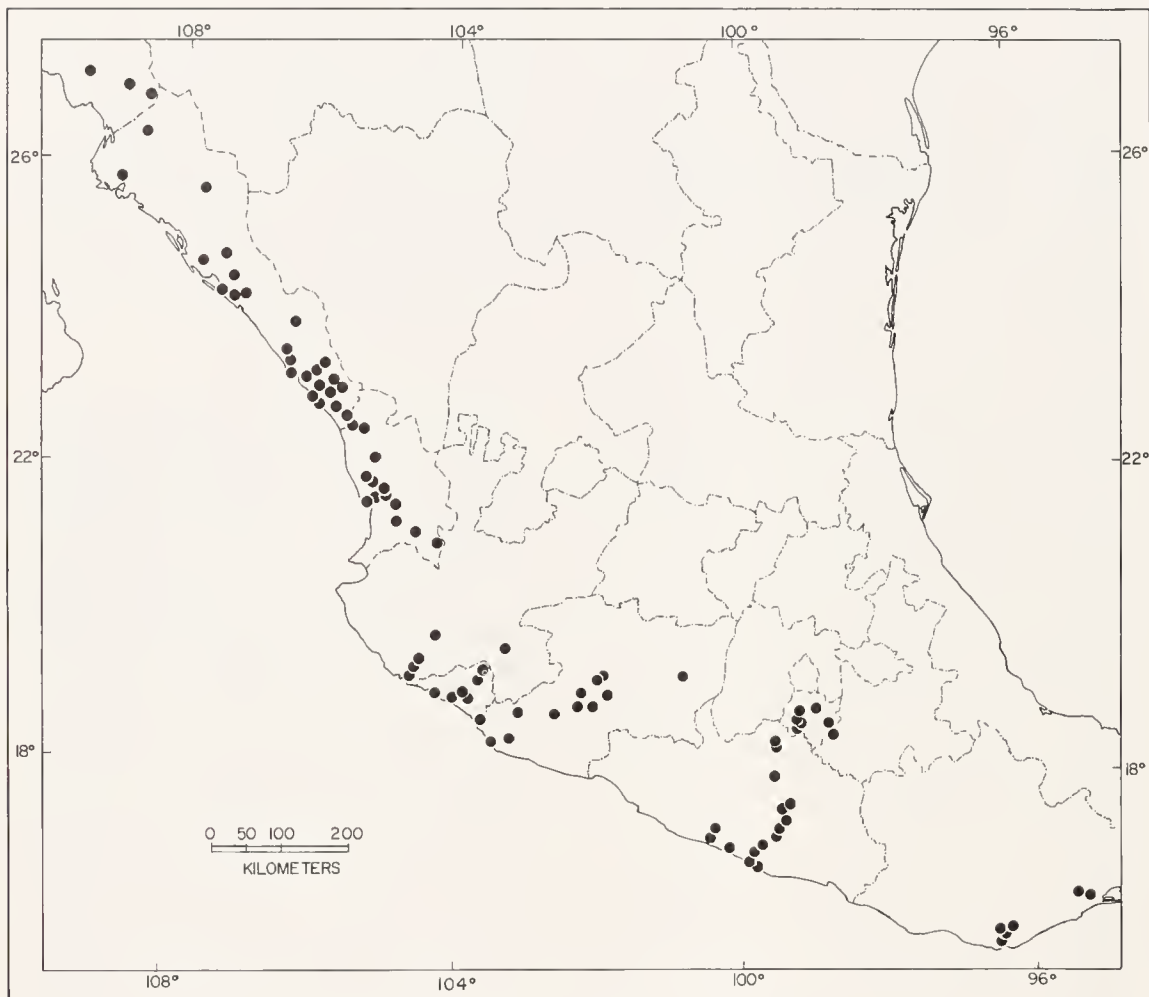


FIG. 26. Distribution of *Pachymedusa dacnicolor*.

not mention *Hyla callidryas*; therefore the consideration of that species as the generotype by original designation, as given by Funkhouser (1957, p. 18) and others is erroneous.

ETYMOLOGY: The generic name is derived from the Greek *aga*, an intensive prefix, and the Greek, *lychnis*, a plant with scarlet flowers. Because of the implied meaning of the generic name it seems likely that Cope was aware that the species known at that time had red eyes.

DEFINITION: Frogs of the genus *Agalychnis* are medium to large in size and have a green dorsum, variously colored flanks that are barred with contrasting colors in some species, and white, yellow, or orange venters.

The pupil is vertical, and the iris is red or yellow. The palpebral membrane is reticulated in all except *A. calcarifer*. The fingers and toes are at least one-half webbed; the terminal discs are large. The first toe is shorter than the second and not opposable to the others. The vocal sac is single, median, and subgular. The skin on the dorsum is smooth; parotoid glands, if present, are poorly developed. There is no integumentary-cranial co-ossification. The tongue is much longer than wide, extensively free posteriorly, and notched anteriorly and posteriorly. Breeding males have horny brown nuptial excrescences on the thumbs. The skull is shallow, and the parietal plane slopes downward anteriorly;

the greatest depth of the skull is less than 40 per cent of the length. The skull is characterized by a large frontoparietal fontanelle, weak quadratojugals (no bony attachment to maxillaries in some species), and moderately developed squamosals having short anterior arms that do not extend more than one-half the distance to the maxillary. The premaxillary has a well-developed, posteriorly inclined alary process. The maxillary bears a moderately deep pars facialis, which at the level of the palatine extends dorsally and connects with the short maxillary process of the nasal. The nasals are large, narrowly separated medially, and separated from the sphenethmoid. The maxillary process of the nasal does not extend to the main axis of the maxillary, but connects with the posterior process of the pars facialis. The sphenethmoid is only moderately ossified. The dentigerous processes of the prevomers are short and situated at an angle to the midline. The pterygoids are robust but do not have a bony attachment to the prootics. The otic region is moderately small. Teeth are present on the premaxillaries, maxillaries, and prevomers, but absent from the palatines and the parasphenoid. The teeth are spatulate and strongly bifid, with a suggestion of a trifold condition in some. The known tadpoles are pelagic types and have mouths that are nearly terminal in position and directed anteriorly; the median part of the upper lip is bare; the rest of the mouth is bordered by two or three rows of papillae. The number of papillae is reduced to one row anterolaterally or medially on the lower lip in some species. The lips are slightly infolded laterally. There are two upper and three lower rows of teeth, and the second upper row is interrupted medially. The spiracle is ventral on the body and sinistral to the midline. The caudal musculature is slender, and the ventral fin is deeper than the dorsal fin. The mating call consists of a single or double note that is short and poorly modulated. The chromosome number is $n=13$ and $2n=26$ (known only in *A. calcarifer* and *callidryas*).

COMPOSITION OF GENUS: Eight species are currently recognized. All are considered to be monotypic, although recognizable geographic variation occurs in *Agalychnis callidryas* and *spurrelli* (see discussions in the accounts of

those species). One species, *Agalychnis craspedopus*, does not occur in Middle America. Of the other seven species, 1437 preserved frogs, 43 skeletons, 62 lots of tadpoles, and 36 preserved clutches of eggs were examined from Middle America.

ANALYSIS OF CHARACTERS: *Agalychnis spurrelli* is the largest species and *saltator* is the smallest; adult males of the former attain snout-vent lengths of 75 mm., and, of the latter, 46 mm. The largest specimen known is a female *Agalychnis spurrelli* having a snout-vent length of 92.8 mm. Females of all species are noticeably larger than the males and have slightly larger tympani. The sizes and proportions of the Middle American species are summarized in table 7.

The taxonomically important external characters are principally those of the hands and feet. Webbing is least extensive in *Agalychnis saltator*, slightly more extensive in *callidryas*, and much more extensive in *annae*, *calcarifer*, *craspedopus*, and *moreletii*; the hands and feet are fully webbed in *litodryas* and *spurrelli* (figs. 27-30). A dermal fold is present on the elbow and knee; this is elongated into a dermal flap in *calcarifer*. Extensive dermal flaps are present on the shank, heel, foot, and forearm of *craspedopus*. In *calcarifer*, *callidryas*, *craspedopus*, and *saltator*, the anal sheath is short, and the anal opening is directed posteroventrally at the level of the middle of the thighs. In the other species the sheath is long, and the anal opening is directed ventrally at the ventral surfaces of the thighs.

The color of, and the pattern on, the flanks and thighs are the most diagnostic features of the coloration (pls. 42 and 43). *Agalychnis litodryas* is unique in lacking pigment on the anterior and posterior surfaces of the thighs and on the flanks. *Agalychnis annae* and *saltator* have uniformly blue flanks and thighs, whereas *moreletii* and *spurrelli* have uniformly orange-yellow flanks and thighs. *Agalychnis calcarifer* and *craspedopus* have orange flanks and thighs with dark vertical bars on both. The most variable species is *callidryas*, in which the flanks vary from pale blue to dark blue or brown; all specimens have vertical or diagonal creamy yellow white bars on the flanks, and specimens from the

TABLE 7
Comparison of Sizes (in Millimeters) and Certain Proportions, with Means in Parentheses, of
Adult Males of the Species *Agalychnis*.

Species	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ S-V L
<i>A. annae</i>	35	57.0-73.9 (67.8)	0.418-0.478 (0.447)	0.341-0.404 (0.447)	0.290-0.328 (0.313)	0.274-0.309 (0.294)	0.431-0.627 (0.563)
<i>A. calcarifer</i>	2	51.9-52.8 (52.4)	0.515-0.520 (0.518)	0.373-0.377 (0.375)	0.323	0.333-0.335 (0.334)	0.760-0.775 (0.768)
<i>A. callidryas</i>	75	44.3-52.1 (48.2)	0.469-0.567 (0.515)	0.331-0.386 (0.357)	0.308-0.352 (0.330)	0.294-0.368 (0.332)	0.400-0.673 (0.524)
<i>A. litodryas</i>	1	70.2	0.523	0.392	0.345	0.307	0.705
<i>A. moreletii</i>	25	55.9-65.7 (60.6)	0.395-0.492 (0.454)	0.332-0.390 (0.367)	0.331-0.344 (0.328)	0.295-0.330 (0.309)	0.603-0.714 (0.670)
<i>A. saltator</i>	19	39.8-46.7 (42.5)	0.467-0.527 (0.505)	0.350-0.395 (0.373)	0.304-0.340 (0.324)	0.293-0.327 (0.310)	0.422-0.555 (0.482)
<i>A. spurrelli</i>	29	48.2-75.6 (62.2)	0.457-0.528 (0.496)	0.365-0.420 (0.394)	0.296-0.328 (0.313)	0.302-0.320 (0.312)	0.462-0.676 (0.568)

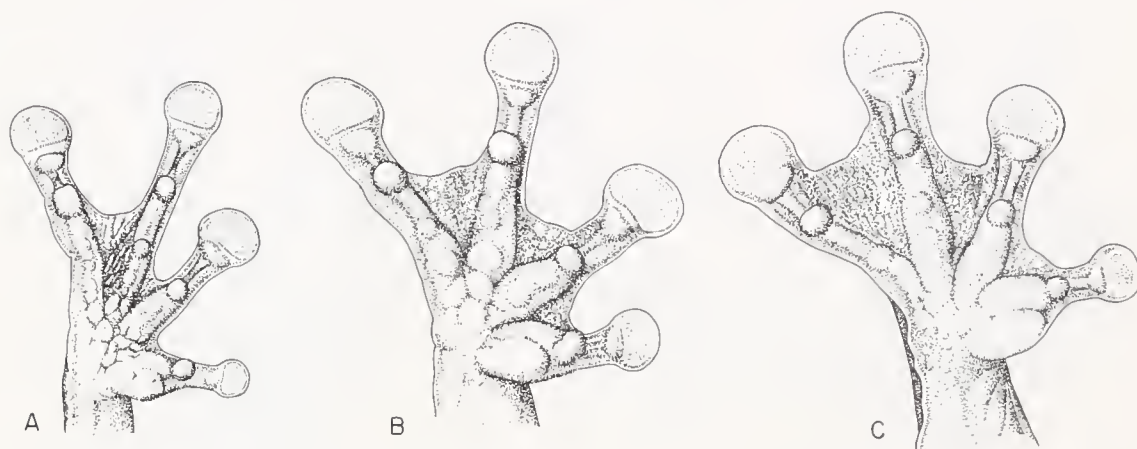


FIG. 27. Hands of three species of *Agalychnis*. A. *A. saltator*, K.U. No. 103805. B. *A. callidryas*, K.U. No. 96140. C. *A. calcarifer*, K.U. No. 77415. $\times 3$.

central part of the range have a longitudinal creamy yellow or white stripe separating the blue flanks from the green dorsum. The color of the thighs in *callidryas* varies from orange to blue. Small, round white spots are present on the dorsum of some specimens of all species except *calcarifer*, *craspedopus*, and *litodryas*. Most specimens of *spurrelli* have black-bordered white spots on the dorsum; this feature of coloration seems to be unique to that species.

The tadpoles of *Agalychnis annae*, *callidryas*, *moreletii*, *saltator*, and *spurrelli* are known. Of these, those of *annae* and *moreletii* are alike and differ from the others in having shorter tails and deeper bodies with slightly protruding snouts (fig. 31). The tadpoles of *callidryas*, *saltator*, and *spurrelli* are more slender and longer. In coloration and structure of the mouths, the tadpoles are nearly alike (fig. 32).

The skulls of five species were studied; those of *Agalychnis calcarifer*, *craspedopus*, and *litodryas* were not examined. Interspecific differences exist in the shape and proportions of the skulls and in the proportions and degree of ossification of certain cranial elements (figs. 33 and 34). The skulls of *annae* and *moreletii* are the deepest, whereas that of *spurrelli* is the shallowest, and those of *callidryas* and *saltator* are intermediate. The skull of *spurrelli* is further distinctive in lacking a bony articulation of the quadratojugal with the maxillary and in having only the posterior

part of the sphenethmoid ossified. The greatest amount of ossification of the sphenethmoid occurs in *moreletii*.

The known mating calls (not known for *calcarifer* and *craspedopus*) consist of a single, or sometimes double note, which is repeated at intervals of a few seconds to several minutes. The calls of *Agalychnis litodryas* and *spurrelli* are a low groan, which is noticeably lower in *spurrelli* than *litodryas*. The calls of the other species are shorter and have the energy spread through the frequency spectrum; furthermore, in these species the last one, or several, pulses are intensified (table 8; pls. 38 and 39).

DISTRIBUTION: The combined distributions of the species of *Agalychnis* include the humid forested lowlands and the humid lower montane forests from central Veracruz and southern Oaxaca, México, southeastward throughout suitable habitats in Central America onto the Pacific lowlands of South America to Esmeraldas Province in northwestern Ecuador. One species, *A. craspedopus*, is known only from the Amazonian lowlands of eastern Ecuador.

DISCUSSION: Prior to Funkhouser's (1957) revision of *Phyllomedusa*, most workers in the present century regarded all Central American phyllomedusines, except *Phyllomedusa lemur*, to be members of the genus *Agalychnis*. Funkhouser (1957) placed *Agalychnis* in the synonymy of *Phyllomedusa*; Goin (1961b) recognized *Agalychnis* and stated: "A recent

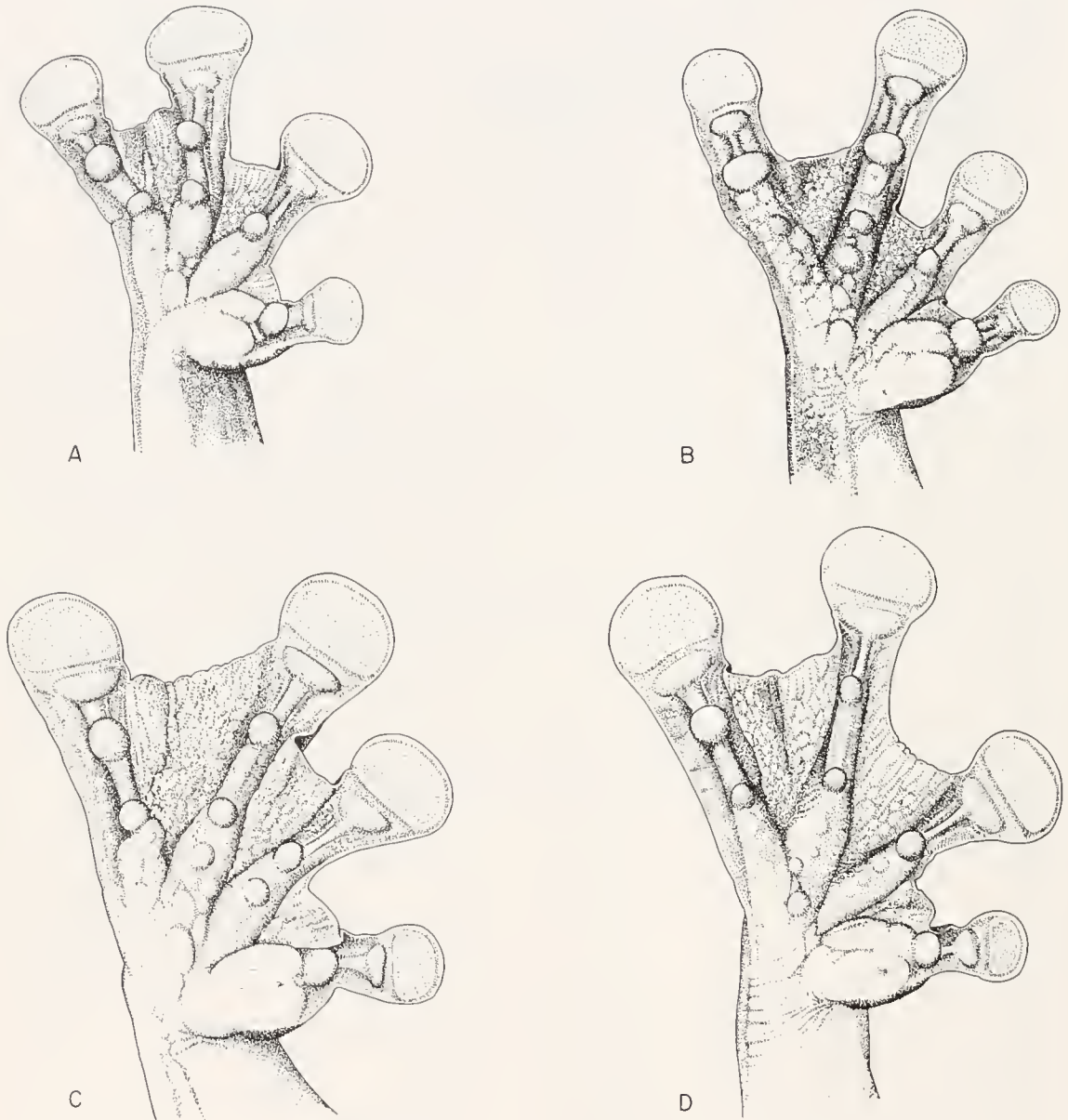


FIG. 28. Hands of four species of *Agalychnis*. A. *A. morcletii*, K.U. No. 57942. B. *A. annae*, K.U. No. 64026. C. *A. spurrelli*, K.U. No. 77499. D. *A. litodryas*, K.U. No. 96149, $\times 3$.

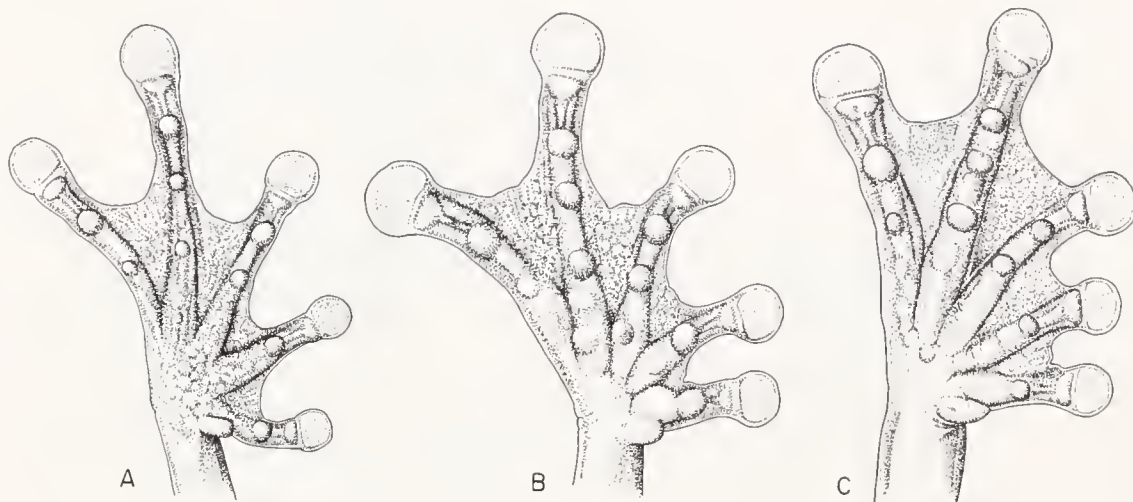


FIG. 29. Feet of three species of *Agalychnis*. A. *A. saltator*, K.U. No. 103805. B. *A. callidryas*, K.U. No. 96104. C. *A. calcarifer*, K.U. No. 77415. $\times 3$.

revision (Funkhouser, 1957) includes *Agalychnis* in *Phyllomedusa*, but the arguments for doing so do not to me seem convincing." Duellman (1968b) recognized *Agalychnis* as distinct from *Phyllomedusa* and proposed that *Agalychnis daenicolor* be placed in a separate genus, *Pachymedusa*.

Within the genus *Agalychnis*, as now recognized, the species can be grouped in four pairs—*saltator* and *callidryas*, *moreletii* and *annae*, *calcarifer* and *craspedopus*, *spurrelli* and *litodryas*. According to Funkhouser's (1957) phylogenetic scheme, *moreletii* and *spurrelli* are primitive, whereas *saltator* and *callidryas* are advanced. Funkhouser attempted to explain the evolution of the species of *Phyllomedusa* by assuming that they evolved from an advanced *Hyla*-like ancestor. Therefore, she placed those species having large fully webbed hands and feet near the base of her phylogenetic scheme and hypothesized that in its evolution the group passed through stages of reduction and eventual loss of webbing to the development of grasping toes. Duellman (1968b) suggested that the evolution of extensive webbing and large adhesive discs probably was not reversed so as to result in generalized hands and feet, from which evolved another kind of arboreal adaptation, the grasping opposable digits. A more reasonable hypothesis is that the evolution of opposable digits took place in a phyletic line

that had as its ancestral stock a frog with generalized hands and feet. If this assumption is correct, *Phyllomedusa* and *Agalychnis* represent two phyletic lines; each evolved independently from a generalized stock, probably not unlike the existing *Pachymedusa*.

It is obvious that *saltator* and *callidryas* are the least specialized species. They have the least modified skulls, the most generalized hands and feet, and lack dermal appendages on the limbs. *Agalychnis moreletii* and *annae* probably were derived from a *saltator*-like ancestor and differentiated from one another through isolation—*moreletii* in the mountains of nuclear Central America and *annae* in the mountains of lower Central America. The *calcarifer*-*craspedopus* line probably evolved through isolation in South America from the main *Agalychnis* stock in Central America. The isolated position of *craspedopus* on the eastern side of the Andes suggests that the *calcarifer*-*craspedopus* stock occupied lowlands on both sides of the mountains. Subsequent differentiation resulted in *craspedopus* in the Amazonian region and *calcarifer* on the Pacific lowlands. *Agalychnis calcarifer* is probably a recent immigrant into lower Central America. Too little is known of the geographic range of *litodryas* to even guess about its differentiation from *spurrelli*.

The phylogeny of the species of *Agalychnis* proposed here assumes a generalized

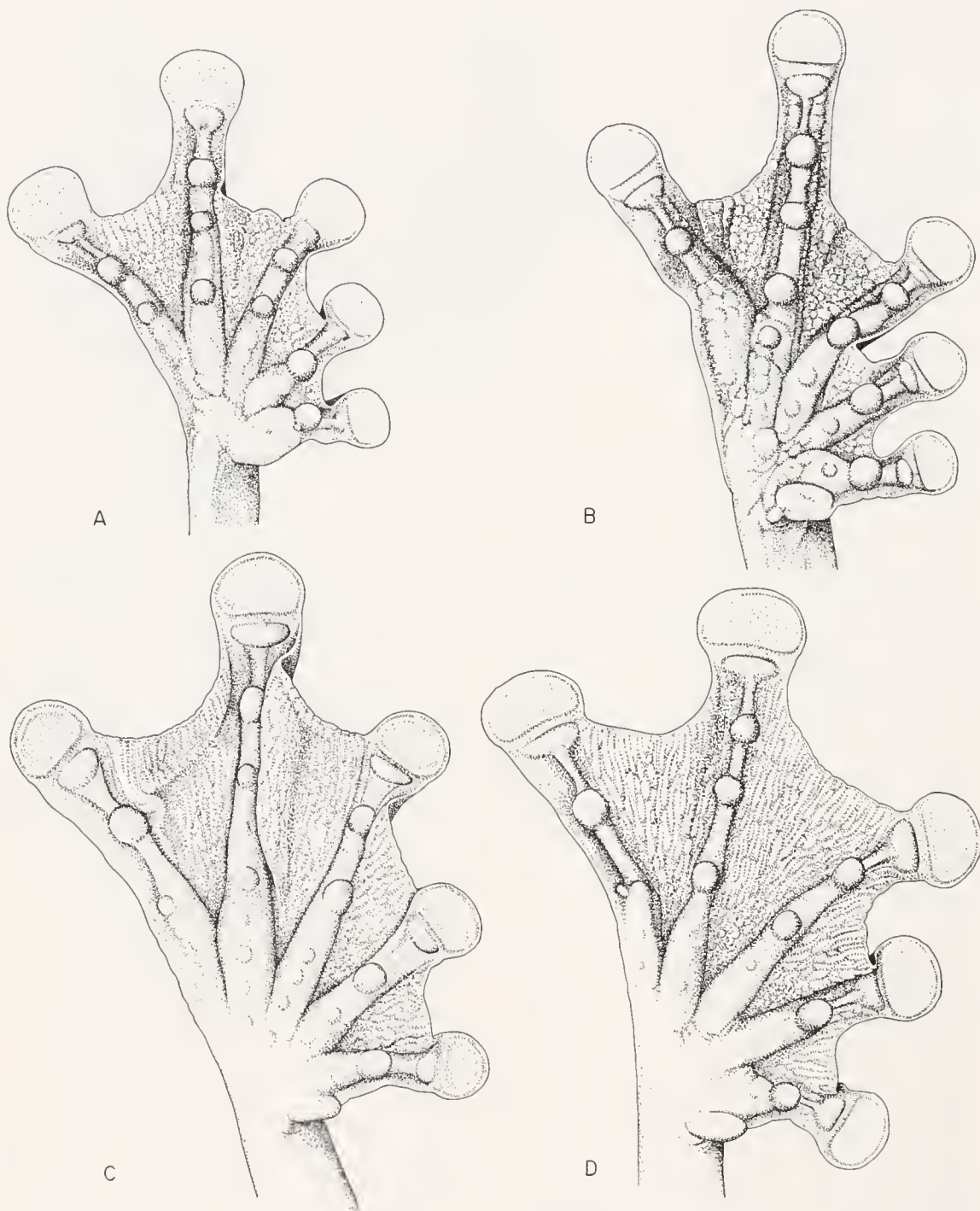


FIG. 30. Feet of four species of *Agalychnis*. A. *A. moreletti*, K.U. No. 57942. B. *A. annae*, K.U. No. 64026. C. *A. spurrelli*, K.U. No. 77499. D. *A. litodryas*, K.U. No. 96149. $\times 3$.

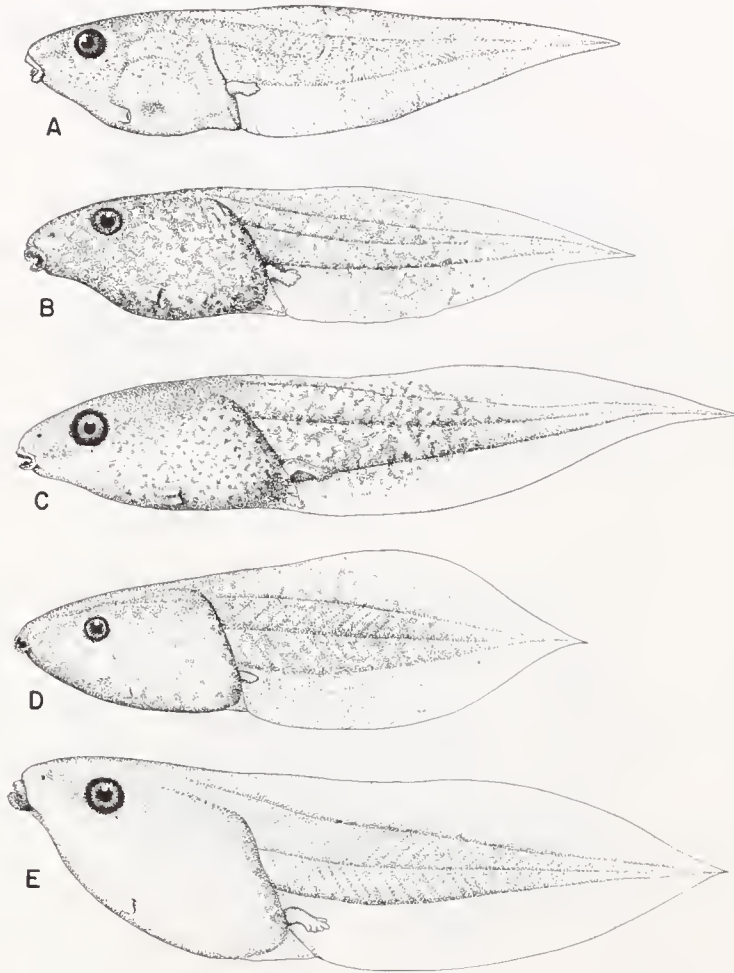


FIG. 31. Tadpoles of five species of *Agalychnis*. A. *A. saltator*, K.U. No. 110130. B. *A. callidryas*, K.U. No. 77630. C. *A. spurrelli*, K.U. No. 104309. D. *A. annae*, K.U. No. 91806. E. *A. moreletii*, K.U. No. 60014. $\times 2$.

hylid ancestral stock having only moderately webbed hands and feet, short anal sheath, and small tympanum, and lacking contrasting markings on the flanks and thighs and dermal appendages on the limbs. From this prototype developed frogs with more extensive webbing and longer anal sheaths. The long anal sheath directed ventrally at the lower level of the thighs possibly is an adaptation for more efficient deposition and fertilization of eggs on leaves. Since blue is a structural color resulting from the absence of lipophores above the guanophores, it is reasonable to assume that blue is a derived color in *Agalychnis*. Thus,

we can assume that the ancestral *Agalychnis* probably had yellow flanks. Starrett's (1960a) description of the ontogenetic development of color pattern in *A. callidryas* provides evidence that the basic colors on the flanks are developed first and that these are followed by the markings. If this is true phylogenetically, as well as ontogenetically, the pattern on the flanks of *callidryas* could have been derived from an ancestral stock colored like *saltator* and the pattern on the flanks of *calcarifer* and *craspedopus* could have been derived from an ancestral stock colored like *spurrelli*.

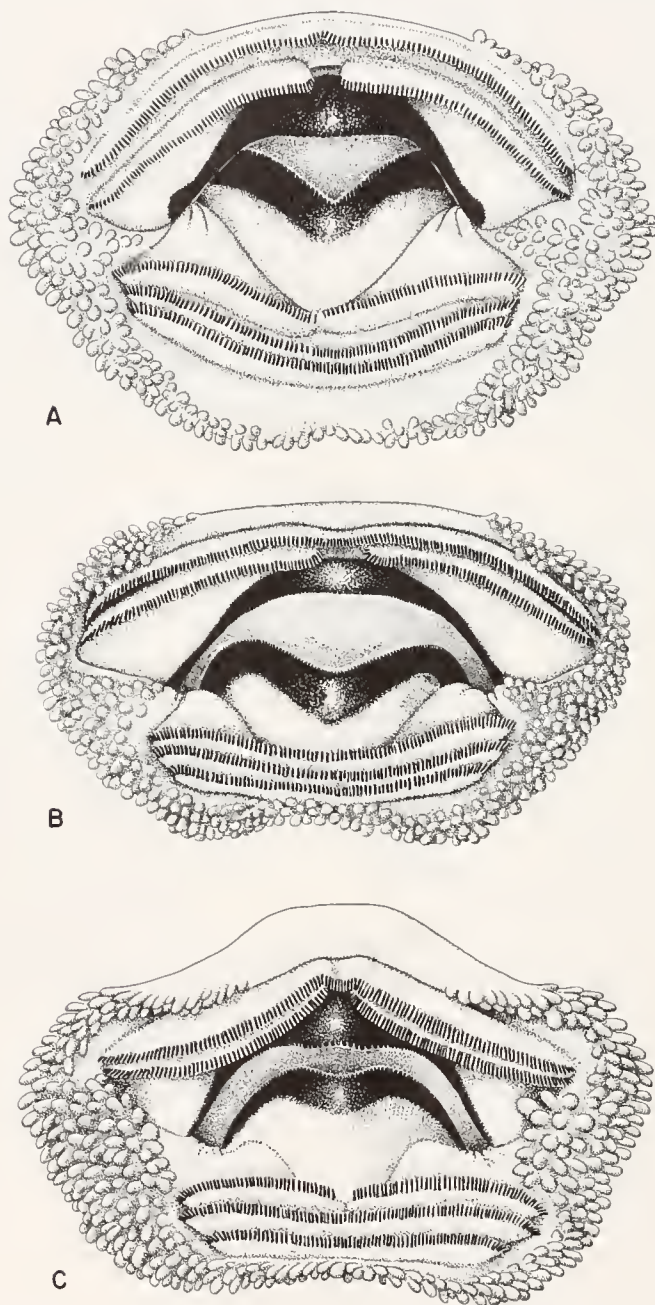


FIG. 32. Mouths of three species of tadpoles of *Agalychnis*.
A. *A. callidryas*, K.U. No. 77630. B. *A. spurrelli*, K.U. No. 104309. C. *A. annae*, K.U. No. 91806. $\times 15$.

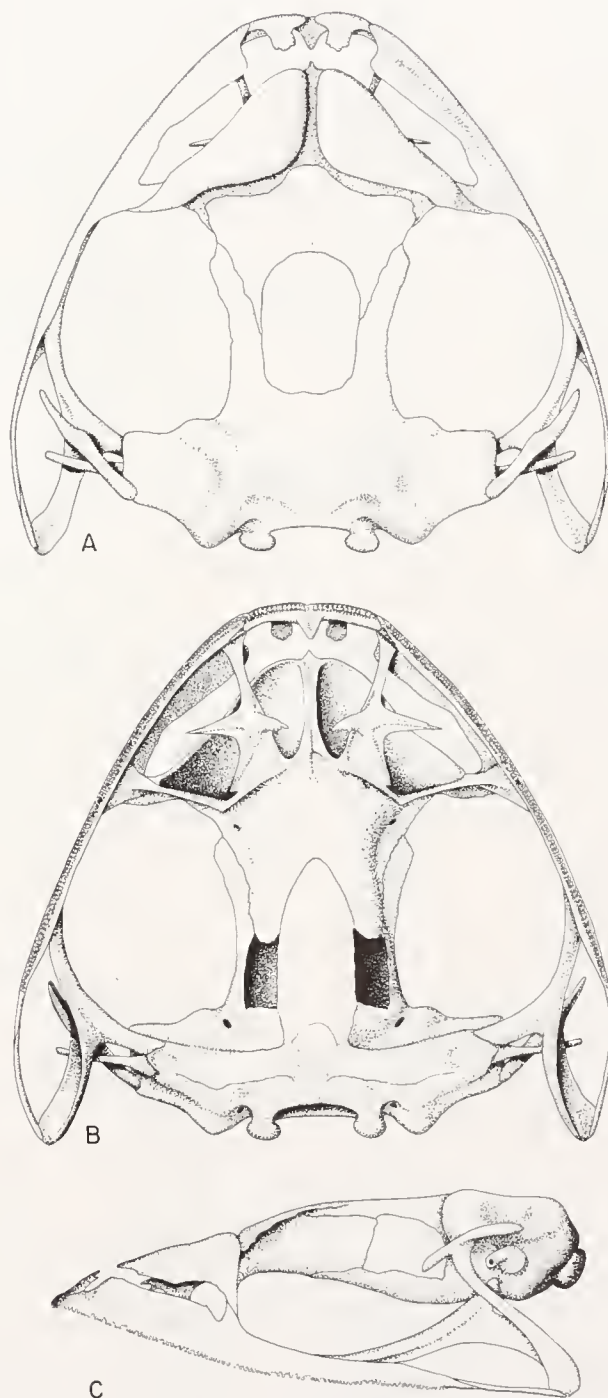


FIG. 33. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Agalychnis callidryas*, K.U. No. 104358. $\times 5$.

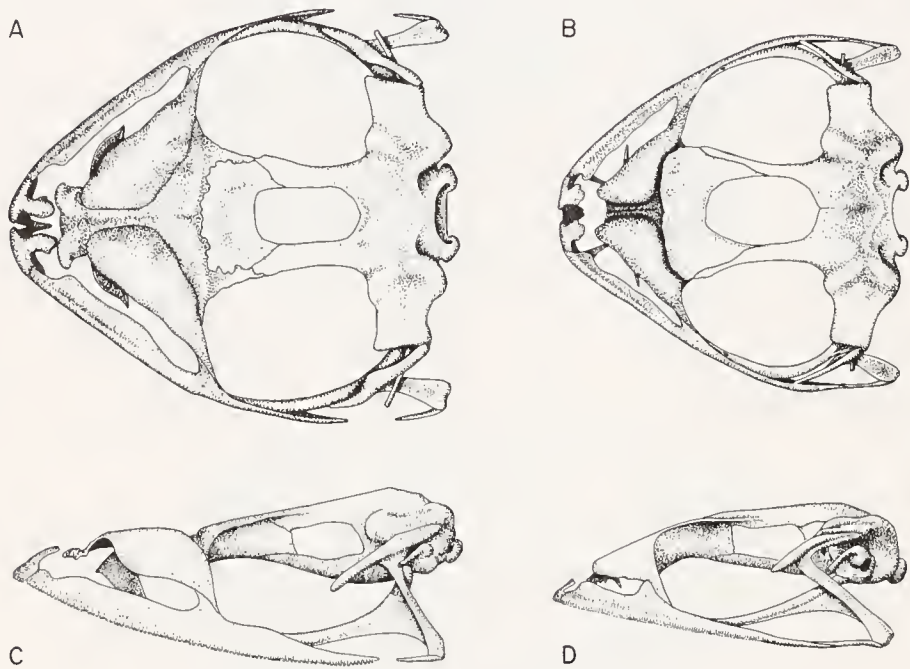


FIG. 34. Dorsal and lateral views of the skulls of two species of *Agalychnis*. A and C. *A. spurrelli*, K.U. No. 77663. B and D. *A. moreletii*, K.U. No. 59852. $\times 3$.

TABLE 8

Characteristics of the Mating Calls, with Means in Parentheses, of the Species *Agalychnis*.

Species	N	Duration (seconds)	Pulses per Second	Fundamental Frequency (cps)	Dominant Frequency (cps)
<i>A. annae</i>	13	0.16-0.44 (0.31)	38-50 (42)	140-185 (161)	1044-1295 (1165)
<i>A. callidryas</i>	25	0.08-0.24 (0.16)	180-200 (189)	165-200 (182)	1488-2400 (1975)
<i>A. litodryas</i>	1	0.15	105	104	1664
<i>A. moreletii</i>	8	0.09-0.27 (0.13)	55-61 (58)	160-185 (172)	1110-1260 (1171)
<i>A. saltator</i>	2	0.08-0.12 (0.10)	105-110 (108)	114-126 (120)	1844-1890 (1867)
<i>A. spurrelli</i>	2	0.34-0.40 (0.37)	60-90 (75)	87-100 (94)	435-700 (568)

Agalychnis saltator Taylor

Agalychnis saltator Taylor, 1955, p. 527, fig. 10 [holotype, K.U. No. 35615 from "4 km. NNE Tilarán, Guanacaste, Costa Rica"; type locality according to collector's field notes and museum catalogue is Finca San Bosco, 5 kilometers north-northeast of Tilarán (fide Duellman and Berg, 1962, p. 189); Edward H. Taylor collector]. Duellman, 1968b, p. 4.

Phyllomedusa saltator: Funkhouser, 1957, p. 36 [transfer of *Agalychnis saltator* Taylor, 1955, to *Phyllomedusa* Wagler, 1830].

DIAGNOSIS: This small species of *Agalychnis* has a dark red eye; the fingers are about one-third webbed, and the toes are about one-half webbed. It differs from all other species in the genus, except *annae*, by having uniformly dark blue or purple flanks and thighs. Furthermore, the dorsum by day is green, with narrow, transverse, darker green lines and at night reddish tan with brown transverse lines. In *annae*, which is much larger, the dorsum is uniformly green by day and night, the eye is orange, and the fingers and toes are about two-thirds webbed. Structurally *saltator* is similar to *callidryas*, but it lacks the vertical white or cream-colored bars on the flanks that characterizes that species and has less webbing on the hands and feet (figs. 27 and 28). *Agalychnis callidryas* does not have a tan dorsum at night. Although some *callidryas* have dark green transverse lines on the dorsum, this species can be distinguished readily from *saltator* in that *callidryas* has orange thighs and vertical cream-colored bars on the flanks.

DESCRIPTION: *Agalychnis saltator* is the smallest species in the genus; males attain a maximum snout-vent length of 46.7 mm. (mean, 19 specimens, 42.5 mm.), and females reach 61.5 mm. (mean, five specimens, 57.0 mm.). In a sample of 10 males from Puerto Viejo, Heredia Province, Costa Rica, the ratio of tibia length to snout-vent length is 0.486 to 0.527 (mean, 0.509); the ratio of foot length to snout-vent length is 0.350 to 0.382 (mean, 0.367); the ratio of head length to snout-vent length is 0.304 to 0.337 (mean, 0.325); the ratio of head width to snout-vent length is 0.293 to 0.327 (mean, 0.311), and the ratio of the diameter of the tympanum to that of the eye is 0.448 to 0.555 (mean, 0.483). Females have proportionately larger tympani;

the tympanum/eye ratio in five females from Puerto Viejo is 0.535 to 0.634 (mean, 0.583).

The head is slightly wider than the body, and the top of the head is flat. In dorsal profile the snout is narrowed and acuminate. In lateral profile, in males, the snout is gently sloping from the eyes to the nostrils and further inclined to the tip of the snout; in females, the snout anterior to the nostrils is bluntly rounded. The nostrils are slightly protuberant and are situated at about three-fourths the distance from the eyes to the tip of the snout. The canthus is rounded and distinct; the loreal region is slightly concave, and the lips are thin and slightly flared. A dermal fold extending from the posterior corner of the eye to a point just posterior to the angle of the jaw conceals the upper and posterior edges of the tympanum. The fold continues as a flap of skin to a point above the insertion of the arm. The tympanum is distinct and situated posterior to the lower one-half of the eye. The tympanum is separated from the eye by a distance equal to about one-half the diameter of the tympanum.

The upper arm is slender, and the forearm is moderately robust. A narrow dermal fold extends across the elbow and along the ventrolateral edge of the forearm to the disc on the fourth finger. The fingers are moderately short and slender and have large discs; the diameter of the disc on the third finger is slightly larger than that of the tympanum in females and about half again as large in males. The subarticular tubercles are small and round, except the distal tubercle on the fourth finger which is larger, flat, and barely bifid in some specimens. The pollex is slightly enlarged and in breeding males bears a horny nuptial excrescence composed of minute spinules. The fingers are about one-half webbed (fig. 27A). The webbing is barely evident between the first two fingers but connects the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third. The web extends from the distal part of the antepenultimate phalanx of the third finger to the base of the penultimate phalanx of the fourth. The hind limbs are slender; the adpressed heels overlap by about one-third of the length of the shank. The tibiotarsal articulation

extends to the anterior corner of the eye. A narrow dermal fold extends along the median edge of the shank, across the heel, and along the ventrolateral edge of the tarsus to the disc on the fifth toe. A weak tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is moderately large, flat, and ovoid. The toes are slender, and the terminal discs are slightly smaller than those on the hands. The sub-articular tubercles are small and round. Supernumerary tubercles are present on the proximal segments of all but the first toe. The toes are about three-fourths webbed (fig. 28A.) The web connects the first two toes at the level of the bases of the penultimate phalanges and extends from that point on the second toe to the base of the antepenultimate phalanx of the third toe. From the base of the penultimate phalanx of the third toe the web extends to the base of the antepenultimate phalanx of the fourth toe and from the middle of the antepenultimate phalanx of the fourth toe to the base of the penultimate phalanx of the fifth.

The anal sheath is short. The anal opening is directed posteroventrally at the level of the middle of the thighs. The skin of the dorsum, chin, chest, and ventral surfaces of the limbs, except proximally on the thighs, is smooth, whereas that on the belly and proximal surfaces of the thighs is granular. A row of large granules extends along the posteroventral edge of the thighs. The tongue is about half again as long as wide, notched anteriorly and posteriorly, and free behind for about one-third of its length. The dentigerous processes of the prevomers are posteromedially inclined ridges between the posterior margins of the long, elliptical choanae. Males have three to five teeth on each process and a total of seven to 10 (mean, 8.6) prevomerine teeth, whereas females have four to six teeth on each process and a total of nine to 12 (mean, 10.6) prevomerine teeth. The vocal slits are situated between the posterolateral corners of the tongue and the angles of the jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration by day is green above with blue flanks and thighs or by night, reddish brown above with blue flanks

and thighs (pl. 42, figs. 1 and 4). By day most individuals are pale green with or without darker green transverse lines on the dorsum and limbs. The flanks and anterior and posterior surfaces of the thighs are purplish blue. The hands, feet, and ventral surfaces of the limbs are pale orange; this color extends onto the anterior and posterior surfaces of the thighs in some males. The throat and anal area are white, and the belly is creamy white. The iris is coppery red, and the palpebral membrane has gold reticulations. In breeding males, the nuptial excrescence is brown. At night the dorsum is reddish tan with brown transverse markings, olive-tan with dark olive-green markings, or dull green with darker green markings. Some specimens have pale yellow spots, narrowly outlined with black on the dorsum.

In preservative, the ventral surfaces are white and the flanks and anterior and posterior surfaces of the thighs are dull purple. The dorsum is pinkish brown to dull blue with darker transverse lines. The dorsal markings are more evident in preserved specimens than in most living individuals. Small white flecks are present on the lower flanks of many specimens, and a small white spot is present at the posterior corner of the eye in some specimens.

TADPOLES: Four tadpoles in developmental stage 28 from Puerto Viejo, Heredia Province, Costa Rica, have body lengths of 9.6 to 10.4 (mean, 10.1) mm., and total lengths of 28.0 to 30.5 (mean, 29.6) mm. Three tadpoles in developmental stage 32 from the same locality have body lengths of 10.8 to 11.5 (mean, 11.1) mm. and total lengths of 33.0 to 36.2 (mean, 34.3) mm. In these specimens the tail length/total length ratio is 0.652 to 0.682 (mean, 0.665).

A tadpole in developmental stage 34 has a body length of 13.8 mm., a total length of 40.2 mm., and a tail length/total length ratio of 0.633. The body is slightly wider than deep; it is widest and deepest posteriorly. The snout in dorsal profile is truncate; in lateral profile the snout slopes gradually from the eyes to the bluntly rounded tip. The nostrils are dorsolateral, about one-third of the distance from the snout to the eyes, and directed anteriorly. The eyes are dorsolateral and di-

rected laterally. The diameter of the eye equals about one-fourth of the greatest depth of the body. The spiracle is ventral and sinistral to the midline; the spiracular opening is at a point about midlength of the body. The mouth is anteroventral and directed anteriorly. The cloacal tube is short and dextral to the caudal fin. The caudal musculature is slender and distally tapered. The depth of the caudal musculature at midlength of the tail is slightly more than the depth of the dorsal fin and noticeably less than the depth of the ventral fin. The dorsal fin is deepest at midlength of the tail and does not extend onto the body. The ventral fin is noticeably deeper than the dorsal fin, has about an equal depth on the anterior two-thirds of the tail, and narrows posteriorly (fig. 31A).

The mouth has a shallow lateral fold. The median part of the upper lip is bare. One or two rows of papillae are present on the rest of the lips. Additional papillae are present in the lateral fold. The upper beak is moderately robust with slender lateral processes. The lower beak is slender and broadly V-shaped. Both beaks have well-developed serrations. There are two upper and three lower rows of teeth. The two upper rows are about equal in length and extend nearly to the lips; the second row is narrowly interrupted medially. The lower rows are progressively shorter from the first to the third; the latter is narrowly interrupted medially.

In preservative the body is pale gray; the caudal musculature is creamy white. Gray reticulations are present on the caudal musculature and fins.

MATING CALL: The call of *Agalychnis saltator* consists of a single, or sometimes double, "clack" repeated at intervals of about 30 seconds to several minutes. Analysis of two calls shows that the duration of the notes is 0.08 and 0.12 (mean, 0.10) of a second. The notes have a pulse rate of 105 and 110 (mean, 108) pulses per second. The fundamental frequency is at 114 and 126 (mean, 120) cycles per second, and the dominant frequency is at 1844 and 1890 (mean, 1867) cycles per second (pl. 38, fig. 1).

NATURAL HISTORY: *Agalychnis saltator* inhabits lowland tropical rain forests where it breeds in temporary and permanent ponds.

Calling males were found at Finca San Bosco, Guanacaste Province, Costa Rica, in August, and calling males and clasping pairs were found at Puerto Viejo, Heredia Province, Costa Rica, in June. At all localities where *Agalychnis saltator* is known, *A. callidryas* also occurs.

REMARKS: Two specimens from Eden Mine, Zelaya Province, Nicaragua (A.N.S.P. Nos. 21131 and 21132), and one from La Castilla, Limón Province, Costa Rica (A.N.S.P. No. 23810) have been misidentified as *Agalychnis callidryas*. All three specimens are clearly *saltator* as evidenced by the small amount of webbing, dark transverse lines on the dorsum, and absence of white vertical bars on the flanks.

ETYMOLOGY: The specific name *saltator* is Latin and means leaper.

DISTRIBUTION: The range of *Agalychnis saltator* extends through the humid Caribbean lowlands from northeastern Nicaragua to

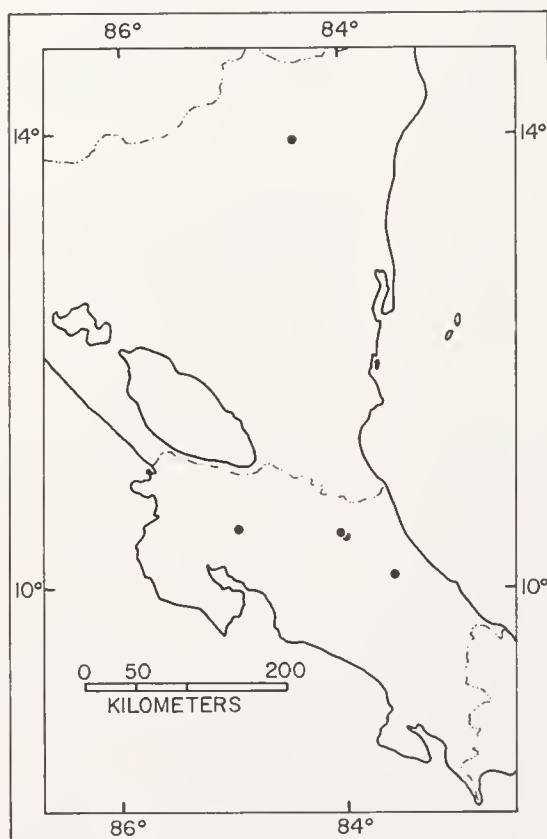


FIG. 35. Distribution of *Agalychnis saltator*.

northeastern Costa Rica (fig. 35) where it occurs on the lowlands and on the lower Caribbean slopes of the highlands to elevations of 780 meters.

See Appendix I for the locality records of the 53 specimens examined.

Agalychnis callidryas (Cope)

Hyla callidryas Cope, 1862, p. 359 [holotype, A.N.S.P. No. 2091 from Darién, Panamá; Captain Field collector; type locality unjustifiably restricted to Córdoba, Veracruz, México, by Smith and Taylor (1950, p. 347)].

Agalychnis callidryas Cope, 1865a, p. 110 [transfer of *Hyla callidryas* Cope to *Agalychnis* Cope, 1864]. Boulenger, 1882a, p. 423. Günther, 1901 (1885-1902), p. 290. Smith and Taylor, 1948, p. 72. Taylor, 1952c, p. 807. Duellman, 1968b, p. 4.

Agalychnis helenae Cope, 1885a, p. 182 [holotype, U.S.N.M. No. 13737 from "Nicaragua"; J. F. Moser collector]. Günther, 1901 (1885-1902), p. 290. Taylor, 1952c, p. 805.

Phyllomedusa helenae: Kellogg, 1932, p. 145 [transfer of *Agalychnis helenae* Cope, 1885a, to *Phyllomedusa* Wagler, 1830]. Funkhouser, 1957, p. 32.

Phyllomedusa (Agalychnis) callidryas: Lutz, 1950b, p. 601 [transfer of *Hyla callidryas* Cope, 1862, to *Phyllomedusa* Wagler, 1830].

Phyllomedusa callidryas callidryas: Funkhouser, 1957, p. 33.

Phyllomedusa callidryas taylori Funkhouser, 1957, p. 34 [holotype, E.H.T. No. 1279 from Tierra Colorado, Veracruz, México; Edward H. Taylor, and Hobart M. Smith collectors]. Stuart, 1963, p. 38.

Phyllomedusa callidryas: Savage and Heyer, 1967, p. 123 [synonymized *Agalychnis helenae* Cope, 1885a, and *Phyllomedusa callidryas taylori* Funkhouser, 1957, with *Phyllomedusa callidryas* (Cope, 1862)].

DIAGNOSIS: This moderate-sized species is distinguished from all other species of *Agalychnis* by having dark flanks with pale vertical bars. The flanks are usually blue, but are brown in some populations, and the vertical bars are white or creamy yellow. The anterior and posterior surfaces of the thighs are unicolor blue or orange. The only other species having vertical bars on the flanks are *A. calcarifer* and *craspedopus*, which have orange flanks with black bars; furthermore, both of these species have dark bars on the thighs. *Agalychnis annae* and *saltator* have uniformly blue flanks lacking vertical bars.

DESCRIPTION: *Agalychnis callidryas* is a moderate-sized, slender species; males attain a maximum snout-vent length of 56 mm., and

females reach 71 mm. The size attained by adults of both sexes varies geographically; in general, specimens from the northern part of the range (México and Guatemala) are the smallest, and those from Nicaragua are the largest (table 9). In a sample of 26 males from Cerro La Campana, Panamá Province, Panamá, the snout-vent length is 44.5 to 50.9 (mean, 47.9) mm., the ratio of tibia length to snout-vent length is 0.477 to 0.532 (mean, 0.510); the ratio of foot length to snout-vent length is 0.340 to 0.386 (mean, 0.363); the ratio of head length to snout-vent length is 0.312 to 0.344 (mean, 0.328); the ratio of head width to snout-vent length is 0.320 to 0.368 (mean, 0.334), and the ratio of the diameter of the tympanum to that of the eye is 0.444 to 0.596 (mean, 0.525). Seven females from the same locality have snout-vent lengths of 54.4 to 66.1 (mean, 62.8) mm. In proportions they differ from the males only in having larger tympani; the tympanum/eye ratio in the females is 0.516 to 0.620 (mean, 0.585) per cent. Little geographic variation in proportions is evident, except that specimens from extreme eastern Panamá have slightly narrower heads (table 10).

The head is slightly wider than the body, except in gravid females, and the top of the head is flat. In dorsal profile the labial border is rounded, and the snout is truncate. In lateral profile, in males, the snout is gently sloping from the eyes to the nostrils and then sharply angled to the snout; in females, the snout anterior to the nostrils is truncate. The nostrils are distinctly protuberant and are situated about four-fifths the distance from the eyes to the tip of the snout in males and even closer to the tip of the snout in females. The canthus is broadly rounded and barely distinct; the loreal region is slightly concave, and the lips are thin and not flared. A thin dermal fold extends posteroventrally from the posterior corner of the eye, covering the upper and posterior edges of the tympanum, to a point just posterior to the angle of the jaw. A heavy dermal flap extends from this point to a point above the insertion of the arm. The tympanum is distinct, situated posterior to the eye, and separated from the eye by a distance equal to about one-half of the diameter of the tympanum.

TABLE 9
Geographic Variation in Size and Coloration, with Means in Parentheses, of Adult *Agalychnis callidryas*.

Population	N	Snout-vent Males	Length Females	Flank Pattern	Number of Bars	Color of Flanks	Color of Thighs
Eastern México	49 ♂, 10 ♀	39.7-49.7 (44.8)	59.9-61.8 (57.8)	10	3-8 (5.0)	Blue	Orange
El Petén, Guatemala	14 ♂, 2 ♀	42.6-48.1 (45.9)	51.6-60.2 (55.9)	10	3-6 (4.5)	Blue	Orange
Caribbean Guatemala	17 ♂, 4 ♀	39.8-51.1 (44.3)	52.7-61.5 (55.9)	10	3-6 (4.2)	Blue	Orange
Northeastern Nicaragua	20 ♂, 5 ♀	48.6-53.1 (50.7)	63.5-66.7 (65.1)	2-6 (3.3)	3-7 (5.1)	Blue	Blue
Southwestern Nicaragua	5 ♂, -----	52.3-58.7 (55.5)	-----	2-10 (4.8)	2-6 (4.5)	Blue	Blue
Northwestern Costa Rica	67 ♂, 19 ♀	43.6-56.4 (49.6)	59.6-70.2 (64.1)	2-6 (2.6)	3-7 (4.8)	Blue	Blue
Northeastern Costa Rica	25 ♂, 5 ♀	48.0-55.6 (48.9)	66.2-70.6 (68.7)	2-4 (2.9)	4-7 (5.2)	Blue	Blue
Southeastern Costa Rica	19 ♂, 4 ♀	44.0-53.7 (47.9)	55.8-68.1 (62.6)	2-5 (3.3)	4-7 (5.4)	Blue	Blue
Bocas del Toro, Panamá	17 ♂, 2 ♀	46.5-53.0 (49.4)	64.1-65.5 (63.6)	3-10 (7.8)	4-7 (5.6)	Blue	Blue and Orange
South-central Costa Rica	6 ♂, 4 ♀	45.1-51.8 (48.3)	54.7-62.5 (59.8)	10	7-11 (8.9)	Blue to Brown	Blue
Golfo Dulce Region, Costa Rica	8 ♂, 1 ♀	45.5-51.8 (48.2)	62.8	9-10 (9.9)	7-11 (8.9)	Blue to Brown	Blue
Cerro La Campana, Panamá	26 ♂, 7 ♀	44.5-50.9 (47.9)	54.4-66.1 (62.8)	4-9 (5.8)	3-8 (5.5)	Blue to Brown	Blue and Orange
Canal Zone, Panamá	28 ♂, 5 ♀	41.4-50.0 (45.6)	62.8-65.5 (63.6)	8-10 (9.7)	4-8 (6.9)	Blue to Brown	Blue and Orange
Tacareuna-Laguna, Darién, Panamá	22 ♂, 10 ♀	47.1-53.1 (50.3)	57.6-67.0 (62.3)	5-10 (9.2)	6-12 (9.1)	Brown	Orange
Río Tuira, Darién, Panamá	12 ♂, 6 ♀	45.8-51.9 (50.3)	62.6-67.2 (64.7)	8-10 (9.4)	6-13 (8.7)	Brown	Orange

TABLE 10
Comparison of Certain Proportions, with Means in Parentheses, in
Five Samples of Adult Males of *Agalychnis callidryas*.

Locality	N	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ S-V L
Toocog, El Petén, Guatemala	14	0.460-0.519 (0.500)	0.331-0.373 (0.352)	0.318-0.352 (0.336)	0.322-0.352 (0.335)	0.450-0.595 (0.524)
Tilarán, Costa Rica	16	0.482-0.533 (0.515)	0.344-0.367 (0.353)	0.315-0.341 (0.329)	0.321-0.345 (0.332)	0.464-0.600 (0.526)
Golfo Dulce Region, Costa Rica	9	0.512-0.567 (0.535)	0.345-0.380 (0.362)	0.308-0.350 (0.332)	0.320-0.355 (0.336)	0.400-0.591 (0.509)
Cerro La Campana, Panamá, Panamá	24	0.477-0.532 (0.510)	0.340-0.386 (0.363)	0.312-0.344 (0.328)	0.320-0.368 (0.334)	0.444-0.596 (0.525)
Río Tuira, Darién, Panamá	12	0.502-0.556 (0.525)	0.338-0.378 (0.353)	0.309-0.352 (0.329)	0.294-0.336 (0.320)	0.428-0.673 (0.530)

The upper arm is slender, and the lower arm is moderately robust. A thin dermal fold crosses the elbow and extends along the ventrolateral edge of the forearm to the disc of the fourth finger. The fingers are short and have moderately large discs; the diameter of the disc on the third finger is equal to, or slightly larger than the tympanum. The subarticular tubercles are large and round, except the distal tubercles on the third and fourth fingers are flattened; the distal tubercle on the fourth finger is bifid in many specimens, and that on the third finger is bifid in many specimens. The pollex is enlarged, and in breeding males bears a nuptial excrescence composed of many horny spinules. The fingers are about one-half webbed (fig. 27B). The webbing extends from the base of the penultimate phalanx of the first finger to the middle of the antepenultimate phalanx of the second, and from the base of the penultimate phalanx of the second finger to the middle of the antepenultimate phalanx of the third. The webbing connects the third and fourth fingers between the distal ends of the antepenultimate phalanges. The hind limbs are slender; when the hind limbs are adpressed, the heels overlap by about one-third the length of the shanks. The tibiotarsal articulation extends to a point between the eye and the tip of the snout. A thin dermal fold crosses the heel and extends along the outer edge of the tarsus to the disc on the fifth toe. The tarsal fold is weak, but extends the full length of the tarsus. The inner metatarsal tubercle is large, slightly rounded, and ovoid. The toes are relatively short and slender; the terminal discs are nearly as large as those on the hand. The subarticular tubercles are small and round. The toes are about two-thirds webbed (fig. 28B). The webbing connects the first and second toes at the bases of the penultimate phalanges and extends from the base of the penultimate phalanx of the second toe to the base of the antepenultimate phalanx of the third. From the middle of the penultimate phalanx of the third toe the web extends to the base of the antepenultimate phalanx of the fourth, and from that point it continues to the base or middle of the penultimate phalanx of the fifth toe.

The anal sheath is short, and the anal

opening is directed posteroventrally at the level of the middle of the thighs. The skin of the dorsum, chin, and ventral surfaces of the limbs, except the thighs, is smooth; the skin of the belly and ventral surfaces of the thighs is granular. The tongue is twice as long as wide, notched anteriorly and posteriorly, and free behind for nearly one-half of its length. The dentigerous processes of the prevomers are posteromedially inclined ridges between the posterior margins of the elliptical choanae. Males have four to six teeth on each process and a total of eight to 11 (mean, 9.7) prevomerine teeth. Females have six to eight teeth on each process and a total of 12 to 16 (mean, 14.0) prevomerine teeth. The vocal slits lie along the inner posterior margin of the jaw. The vocal sac is single, median, subgular, and not noticeably distensible.

The general coloration consists of a green dorsum, creamy white venter, and dark flanks with vertical or diagonal creamy yellow bars (pl. 42, figs. 2 and 5). The dorsal surfaces of the head, body, hind limbs, forearm, fourth fingers, and fifth toes are leaf green, varying in some individuals to darker green. Some specimens, especially those from Nicaragua and Costa Rica have faint, narrow, dark green transverse lines on the dorsum. The throat and belly are creamy white. The hands and feet, with the exception of the outer digits on each, are orange. A white line is present on the outer edge of the tarsus and on the outer edge of the forearm. In some specimens from Nicaragua and the Caribbean lowlands of Costa Rica a thin white line usually is present on the edge of the upper eyelid. The iris is red, and the palpebral membrane is reticulated with gold; the nuptial excrescences are dark grayish brown.

The colors of the flanks and thighs, and the pattern on the flanks varies geographically (fig. 36, table 9). The general trend in variation is an increase in the numbers of bars on the flanks from north to south. For example, 69 specimens from Oaxaca and Veracruz, México, have 3 to 8 (mean, 5.0) bars on each flank, whereas 50 specimens from Darién Province, Panamá, have 6 to 13 (mean, 9.0) bars. In most specimens from México south-eastward to Bocas del Toro Province, Panamá,

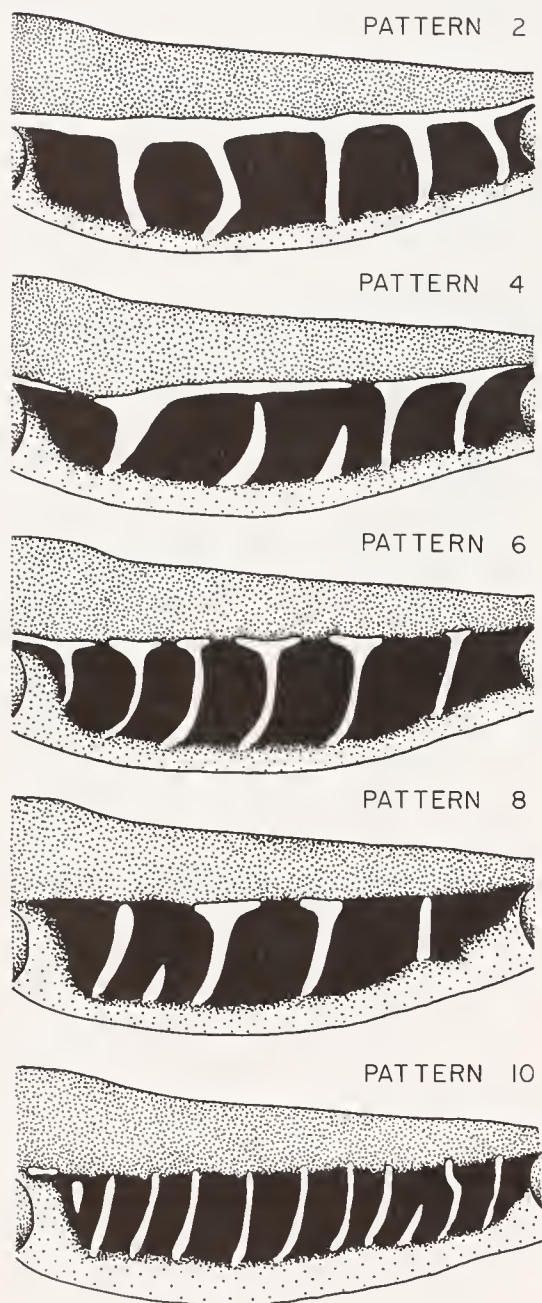


FIG. 36. Flank patterns in *Agalychnis callidryas* (somewhat diagrammatic). Pattern 2. K.U. No. 103786. Pattern 4. K.U. No. 77434. Pattern 6. K.U. No. 77456. Pattern 8. K.U. No. 77441. Pattern 10. K.U. No. 77494.

the cream bars are broader than in those specimens from the Golfo Dulce region of Costa Rica and from central and eastern Panamá, although in some individuals the bars are narrow. In the middle part of the range (Caribbean lowlands of Nicaragua and Costa Rica) the dark blue flanks are separated from the green dorsum by a longitudinal creamy yellow line, which in most specimens connects the upper edges of the vertical bars. This longitudinal stripe is absent in specimens from the northern part of the range (México southward through Honduras) and from the south (Panamá and Pacific lowlands of Costa Rica). In some specimens from the middle part of the range the longitudinal stripe either is discontinuous or is not fused with all of the vertical bars.

The variation in pattern on the flanks (fig. 36) was coded, and the ranges and mean values for 15 samples were calculated (table 9). In some specimens, the pattern on the left and right flanks were different; in these cases an intermediate value was assigned. For example, a specimen having pattern 2 on one flank and pattern 4 on the other was given a value of 3. Examination of table 9 reveals that the lowest values (greatest number of specimens having pattern 2) occur in Nicaragua and the Caribbean lowlands of Costa Rica. In either direction the values increase to, or near to, pattern 10.

In addition to pattern, the color of the flanks varies geographically. In México and Guatemala the flanks are pale blue to dark blue, and in Nicaragua and the Caribbean lowlands of Costa Rica and western Panamá the flanks are dark blue to purple. On the Pacific lowlands of Costa Rica and in central Panamá (Cerro La Campana and Canal Zone) the flanks are dull blue to purplish brown, and in eastern Panamá they are brown. The anterior and posterior surfaces of the thighs, and the ventral surfaces of the thighs and shanks are dark blue in specimens from Nicaragua and the Caribbean lowlands of Costa Rica, whereas elsewhere in the range these surfaces are predominantly orange. Some specimens from Bocas del Toro Province, Canal Zone, and Cerro La Campana, Panamá Province, in Panamá have some blue proximally on the anterior and posterior sur-

faces of the thighs; otherwise, the thighs are orange.

Small white spots are present on the dorsum of the body in many specimens. In those specimens having spots, the number of spots varies from 1 to 22. The percentage of individuals having spots varies from 44 to 62 in three samples from the northern part of the range (eastern México, Guatemala, and Honduras) and from 42 to 75 in Nicaragua and the Caribbean lowlands of Costa Rica the percentage varies from zero to 30. Although the majority of specimens from Nicaragua and the Caribbean lowlands of Costa Rica lack white spots, 16 per cent of the 169 specimens from that region have five white flecks on the dorsum.

In preservative the dorsum is blue, and the venter is white. The flanks are dark blue or lavender with white bars. The thighs are blue or creamy white.

TADPOLES: Seven hatchling tadpoles from Toocog, El Petén, Guatemala, have total lengths of 7.2 to 7.8 (mean, 7.4) mm., and four hatchlings from 22 kilometers south of Managua, Nicaragua, have total lengths of 11.4 to 12.7 (mean, 12.1) mm. Nine tadpoles in stages 27 to 32 from Toocog have body lengths of 8.7 to 9.3 (mean, 9.1) mm. and total lengths of 21.8 to 26.1 (mean, 23.4) mm., whereas 12 tadpoles in the same developmental stages from Barro Colorado Island, Panamá, have body lengths of 14.7 to 17.9 (mean, 16.1) mm. and total lengths of 31.0 to 40.2 (mean, 36.9) mm. Two tadpoles in stage 41 from Barro Colorado Island, Panamá, have body lengths of 17.5 and 19.3 mm. and total lengths of 48.0 and 53.0 mm.

A typical tadpole in developmental stage 34 has fully developed mouth parts but has undergone no external changes, except for the development of limb buds (fig. 31B). The body is slightly deeper than broad. It is deepest posteriorly and widest just behind the eyes. The snout in dorsal profile is truncate; in lateral profile it is acuminate and slightly dorsal to the midline. The nostrils are dorsolateral, about one-third of the distance from the snout to the eyes, and directed anteriorly. The eyes are dorsolateral and directed laterally. The diameter of the eye equals about one-fourth of the greatest depth of the body.

The spiracle is ventral and sinistral to the midline; the spiracular opening is at a point about midlength of the body. The mouth is anteroventral and is directed anteriorly. The cloacal tube is short and dextral to the caudal fin. The caudal musculature is slender and distally gradually tapers nearly to reach the tip of the fin. The depth of the musculature at midlength of the tail is slightly more than the depth of the dorsal fin and about equal to one-third of the depth of the tail. The dorsal fin is deepest at midlength of the tail and does not extend onto the body. The ventral fin is noticeably deeper than the dorsal fin, has about equal depth on the anterior two-thirds of the tail, and narrows posteriorly.

The mouth has a shallow lateral fold. The median part of the upper lip is bare; lateral to the bare part of the upper lip and on the median part of the lower lip one row of papillae is present. Otherwise, two or three rows of papillae are present on the lips. Laterally, additional papillae are medial to the fringing papillae. The upper beak is moderately robust and forms a broad arch; the lateral processes are slender and barely expanded distally. The lower beak is rather slender. Both beaks have well-developed, blunt serrations. There are two upper and three lower rows of teeth. The two upper rows are about equal in length and extend nearly to the papillae; the second row is interrupted medially. The lower rows are continuous; the first and second rows are nearly as long as the upper rows, whereas the third row is slightly shorter (fig. 32B).

The snout, top of head, and dorsolateral surfaces of the body are olive-gray; the sides and venter are bluish gray with olive-brown flecks. In some tadpoles, the belly has a golden cast. The caudal musculature is grayish tan and the caudal fins are transparent; both are flecked with dark gray. In late stages the dark pigment expands to form bold reticulations on the tail and a uniform olive-brown dorsum. The iris is bronze.

The most noticeable variation in tadpoles is in the arrangement of labial papillae. Most specimens agree with the preceding description, but some have two rows of papillae lateral to the bare median part of the upper lip and two rows medially on the lower lip. In

some specimens, the first lower tooth row is narrowly interrupted. The extreme condition in number of rows of papillae is that illustrated and described by Duellman (1963b).

MATING CALL: The call consists of a single, or sometimes double, note—"chock," repeated at intervals of eight seconds to about one minute. Analysis of recordings and notes taken in the field revealed that some individuals emitted a series of calls in which the double notes were more numerous than the single notes, but no individual emitted more than three consecutive double notes, whereas some individuals emitted only single notes. The duration of the notes is 0.08 to 0.24 (mean, 0.16) of a second. The notes are characterized by a pulse rate of 180 to 200 (mean, 189) pulses per second. The notes are characterized by 11 to 35 (mean, 20.8) pulses; the last few pulses are intensified. The fundamental frequency falls between 165 to 200 (mean, 182) cycles per second, and the dominant frequency lies at 1488 to 2400 (mean, 1975) cycles per second (pl. 38, fig. 2).

There is some noticeable geographic variation in the calls; especially evident is a decrease from north to south in the pulse rate and a corresponding lowering of the fundamental and dominant frequencies (table 11).

NATURAL HISTORY: *Agalychnis callidryas* inhabits forested regions where it breeds in temporary and permanent ponds during the rainy season. In the drier parts of the range, where the rainy season is short (for example, Campeche and southern Veracruz, México,

and northern El Petén, Guatemala), the breeding season is shorter than in areas characteristically having a long rainy season. Calling males were taken in October, November, and March in Bocas del Toro Province, Panamá.

Numerous workers (Dunn, 1931b; Breder, 1946; Pyburn, 1963; and Duellman, 1963b) have presented data on the breeding habits of this species. The observations presented in these papers are incorporated here with my own unpublished observations.

Daytime and dry season retreats apparently are in trees. Stuart (1958, p. 18) reported finding the frogs in palm fronds in the dry season at Tikal, El Petén, Guatemala, and I obtained one individual from a bromeliad at Laguna Monte Alegre, Alajuela Province, Costa Rica. At several different localities (Toocog, El Petén, Guatemala, and Laguna, Tacarcuna, and Río Tuira, Darién Province, Panamá) frogs were observed descending trees at dusk. At Toocog the frogs descended a large vine-covered tree standing in the water. At Laguna and Río Tuira the frogs were in large trees on slopes near the breeding ponds. On several evenings at Laguna, the breeding area was under observation prior to dusk. Shortly after sunset *Agalychnis callidryas* was heard to call from heights in the trees. Some of the calls were the normal mating calls, but most were a series of notes which might correspond to the rain-call of some frogs (pl. 30, fig. 3). In each observation, within about five minutes most of the

TABLE 11
Variations in the Mating Call of *Agalychnis callidryas*.
(The means are given in parentheses)

Locality	N	Duration of Notes (seconds)	Pulse Rate (seconds)	Fundamental Frequency (cps)	Dominant Frequency (cps)
Oaxaca, México	6	0.10-0.20 (0.16)	190-195 (193)	168-200 (183)	2016-2400 (2185)
El Petén, Guatemala	5	0.19-0.23 (0.22)	180-195 (188)	174-192 (184)	1990-2293 (2097)
Buenos Aires, Costa Rica	3	0.16-0.24 (0.19)	190-200 (193)	174-191 (182)	1910-2088 (2000)
Canal Zone, Panamá	9	0.08-0.14 (0.11)	180-195 (182)	165-191 (176)	1488-1914 (1734)
Darién, Panamá	2	0.17-0.19 (0.18)	180	160-182 (171)	1920-2002 (1961)

frogs ceased calling. Then followed a period of time in which the frogs descended to the pond and began producing the mating call. The function of the rain call is not known, although Blair "1958" [1959] and Bogert (1960) suggested that these calls in some *Hyla* in southeastern United States and México might have a territorial function. In the case of *Agalychnis callidryas* the calls at dusk seem to be more of an "awakening" vocalization. On two occasions these calls have been heard at dawn, after the frogs had left the pond and ascended trees. After a few minutes of vocalizations from the trees the frogs became silent as the sky lightened. This vocalization at dawn adds support to the idea that these calls have a territorial function, but observations are too incomplete at this time to do more than raise questions concerning this phase of the frogs' behavior.

Males call from trees and bushes above, or at the edge of, the water. Usually they sit perpendicular to the axis of the branch or vine on which they are perched. The perches usually are one to three meters above the water, but some males have been observed 8 to 10 meters above the water. At most breeding sites the males seem to be well spaced about the pond, but in some restricted sites they were found to be crowded. Even though some individuals were calling from adjacent positions on the same branch, no aggressive behavior was noted.

Gravid females have been observed approaching calling males, which usually see the female only after she has approached to within a few centimeters of the male. Once the male sees the female, he walks to her and clasps her. Extremes in this behavior have been noted. One female walked about one meter out on a limb and approached a male calling from a position perpendicular to the limb. The male continued to call as the female placed a hand on his back and did not take notice of her until after she had crawled over him and proceeded a short distance beyond him. On three occasions males were observed to clasp other males. In two instances the clasped male called (apparently the normal mating call), and the clasping male released his hold. In a third instance the clasped male jumped (with the clasping

male on his back) into the water about two meters below; upon impact the clasping male released his hold.

Amplexus is axillary. My observations support those of Pyburn (1963, p. 158) on the placid nature of the males once they are in amplexus. Usually the males adhere closely to the backs of the females and often close their eyes. A notable exception to this behavior was a clasping pair observed in a pond 3 kilometers north of Donaji, Oaxaca, México. A distinctly odd-sounding *Agalychnis* call was heard; it was traced to a male in amplexus.

Females carry the males on their backs and climb or walk about in trees and bushes apparently in search of a suitable egg-deposition site. Fouquette ("1966" [1967], p. 170) observed a clasping pair in the water in a ditch and suggested that amplexant pairs move first to water and then to vegetation above the water for oviposition. The eggs are deposited usually on leaves that are over the water; sometimes the eggs are suspended from vines or branches, and one clutch was adherent to a tree trunk. Pyburn (1962, p. 158) did not observe attempts by the frogs to curl the leaves around the eggs. I observed leaves curled about eggs as they were being deposited at Teapa, Tabasco, México, and on the Cerro La Campana, Panamá Province, Panamá. In both cases the leaves were partly curled when I made my first observations, and I saw no activity on the part of the frog that resulted in curling the leaves. Several clutches of eggs completely encircled by leaves have been found. I suspect that this is a result of attachment of the eggs to particular kinds of leaves and not the result of the frogs curling the leaves as stated by Goin (1960a, p. 438).

Pyburn (1963, p. 159) reported 40 to 68 (mean, 51) eggs in nine clutches at Encinal, Veracruz, and Duellman (1963, p. 226) found 14 to 44 (mean, 29) eggs in 26 clutches at Toocog, Guatemala. Fifteen clutches at Cerro La Campana, Panamá, contained 29 to 78 (mean, 43) eggs, and 11 clutches at the Río Tuira at the Río Mono, Panamá, contained 11 to 39 (mean, 26) eggs. Three gravid females from Toocog contained 39, 78, and 91 ovulated eggs, and four females from Cerro La Campana contained 53, 79, 96, and 108 ovulated eggs. In addition to the

ovulated eggs two of the females from Toocog and all of those from Cerro La Campana contained about equal numbers of ovarian eggs that were about one-half of the size of the ovulated eggs. Both ovarian and ovulated eggs were pale green. The disparity in the numbers of ovulated eggs and those making up the clutches suggests that each clutch represents only part of the egg complement of a given female. Whether different clutches deposited by a single female represent matings with one or more males is not known. Furthermore, the presence of large ovarian eggs in females containing ovulated eggs indicates a strong possibility that the females ovulate twice in one breeding season.

The eggs are rather evenly distributed near the surface of the mass of clear jelly. In early stages of development the yolk is pale green, and the animal pole is brown. In later stages the yolk is yellow. Duellman (1963b, p. 226) briefly described eggs of *Agalychnis callidryas* from Toocog, Guatemala. He reported that in eggs in yolk plug stage the average diameter of the embryos was 2.3 mm. and that of the inner envelopes, 3.4 mm. Pyburn (1963) described and illustrated in detail the embryonic development of this species at Encinal, Veracruz; the reader is referred to this paper for the descriptive embryology.

Hatching is accomplished by vigorous wriggling by the tadpole, which thereby ruptures the egg membranes and drops to the water below. Duellman (1963b, p. 227) observed one clutch of 19 eggs hatching within three minutes. Obstacles, such as branches or emergent vegetation, sometimes impede the fall to the water, and because of placement of some clutches, the tadpoles fall onto the ground. Pyburn (1963, p. 160) stated: "Newly hatched tadpoles of *callidryas* are capable of flipping themselves about on a dry surface by vigorous contractions of the tail musculature, and could conceivably get to standing water if they fell within a few inches of the water's edge."

The newly hatched tadpoles apparently sink to the bottom of the pond, and one or two minutes elapse from the time they drop into the water until they reappear at the surface. The tadpoles characteristically orient

themselves head up near the surface of the water. Large tadpoles were observed to congregate in open sunny parts of the pond at Toocog, Guatemala.

Metamorphosing young have been found throughout the latter part of the rainy season and into the dry season. Stuart (1958, p. 18) found young in February at Tikal, Guatemala. Pyburn (1963, p. 168) raised the eggs of *Agalychnis callidryas* and succeeded in rearing one individual to metamorphosis in 79 days after hatching. His metamorphosed young had a snout-vent length of 18.5 mm. Twenty young from 22 kilometers south of Managua, Nicaragua, have snout-vent lengths of 19.7 to 21.9 (mean, 20.6) mm., and four from Laguna, Darién Province, Panamá, have snout-vent lengths of 19.2 to 19.7 (mean, 19.5) mm. Pyburn (1963, p. 168) noted that the young had a green dorsum, a yellow iris, and lacked vertical bars on the flanks. Specimens from Panamá were reddish brown at night but changed to pale green by day. They had a yellowish gold iris and lacked bars on the flanks. Starrett (1960a, p. 30) raised recently metamorphosed young from Los Diamantes, Limón Province, Costa Rica. Regarding the development of the color pattern she stated: "The green adult coloration did not appear until resorption of the tail had begun. At about the time that the tail disappeared the white lateral stripe was noticeable, but the vertical stripes and purple color on the lower sides did not appear for several weeks. The vertical pupil of the froglet was noticed when the froglet crawled out of the water, but the red color did not become apparent for two weeks. Then it took several days for the eye to become completely red as the coloration spread inward over the iris from the periphery where it first became evident." In the series of young from 22 kilometers south of Managua, Nicaragua, some individuals have a longitudinal white stripe present along the length of the flank, whereas in others the stripe is present only posteriorly. None has vertical bars. Recently metamorphosed young have only slight webbing between the fingers; the toes are about one-third webbed.

REMARKS: Most workers in the present century, prior to Funkhouser (1957), recog-

nized two taxa of Central American *Agalychnis* with pale vertical or diagonal bars on blue flanks; *A. helenae* was characterized by the presence of a longitudinal white line on the flanks and blue thighs, whereas *A. callidryas* had orange thighs and lacked the longitudinal line. Funkhouser (1957) named the Mexican and Guatemalan populations *A. callidryas taylori*, which she diagnosed as differing from the nominate subspecies in size and certain proportions.

Savage and Heyer (1967) partially analyzed the variation in these three taxa and concluded that only one species was represented. Furthermore, they argued that the variation was such as to preclude the recognition of subspecies. Savage and Heyer carefully analyzed the variation in the color pattern on the flanks and the size of adults and briefly mentioned the color of the thighs; their conclusions were based principally on the pattern. When the variation in the color of the flanks and the number of bars on the flanks are also taken into consideration (table 9), the correlation of variation in two or more characters takes on a different aspect than that presented by Savage and Heyer. They stated that on the basis of pattern the specimens from the Pacific lowlands of Costa Rica and western Panamá are like those of the Mexican, Guatemalan, and Honduran specimens. The significance of the similarity in pattern is diminished by the differences in the colors of the flanks and the numbers of vertical bars present in the two samples (table 9).

No specimens have been examined that are intermediate between the northern populations (orange thighs and no longitudinal white stripe on the flank) and the Nicaraguan and Costa Rican populations (blue thighs and a white stripe on the flank). A broad hiatus of about 300 kilometers separates the southeasternmost locality of the northern population from the Nicaraguan population. The absence of specimens from the intervening area probably is due to lack of collecting and not to the absence of the frogs in that area.

Many specimens from Bocas del Toro Province and some specimens from the Canal Zone and Cerro La Campana, Panamá, have blue on the proximal surfaces of the thighs,

which otherwise are orange. Furthermore, a pattern of T-shaped bars, some of which are connected dorsally, on the flanks occurs in these specimens. Therefore, in these characters the frogs are intermediate between the Nicaraguan-Costa Rican populations and those in eastern Panamá. Frogs having characteristics of the Caribbean populations are found on the Pacific slopes only on Cerro La Campana, which has a herpetofauna composed of many species that predominantly range only on the Caribbean slopes. Other samples from the Pacific lowlands of Panamá and Costa Rica are characterized by many vertical bars (lacking a dorsal connection), brown flanks, and orange thighs.

Several taxonomic arrangements of the populations are possible. Savage and Heyer (1967) argued strongly against taxonomic recognition of any of the populations. Equally valid evidence supports the recognition of three taxa—a northern population from Honduras to México, a central population in Nicaragua and Costa Rica, which apparently intergrades with a third population occurring in Panamá and on the Pacific lowlands of Costa Rica. Since the evidence for the taxonomic recognition of the populations is not much more impressive than Savage and Heyer's evidence for regarding all of the populations as one taxon, no formal taxonomic changes should be proposed until specimens are obtained from the Honduran hiatus. Presumably specimens from that area will provide the necessary evidence to determine whether or not the northern population intergrades with that in Nicaragua.

ETYMOLOGY: The specific name *callidryas* is derived from the Greek *kallos*, meaning beautiful, and the Greek *Dryas*, a tree nymph.

DISTRIBUTION: The range of *Agalychnis callidryas*, as now recognized, includes the Atlantic slopes and lowlands from southern Veracruz and northern Oaxaca, México, south-eastward to northern Honduras and thence, presumably continuous, southward on the Caribbean slopes and lowlands to the Canal Zone, Panamá, east of which the species occurs on the Pacific lowlands (fig. 37). A disjunct population occurs on the Pacific lowlands from the area between Esparta and San Ramón, Costa Rica, southeastward to extreme

western Chiriquí Province, Panamá. Old records for the species in Yucatán, México are based on specimens obtained at cenotes. It is doubtful if the species is widely distributed in the Yucatan Peninsula. I heard, but did not obtain, individuals at Felipe Carrillo Puerto, Quintana Roo. The species is characteristic of the lowlands throughout its range, but does ascend the slopes of mountains in many places. It has been taken at 740 meters on Cerro La Campana, Panamá, 780 meters at Silencio, Costa Rica, 820 meters at Laguna, Panamá, and at 960 meters at Finca Tepeyac, Nicaragua.

See Appendix 1 for the locality records of the 969 specimens examined.

Agalychnis moreletii (Duméril)

Hyla moreletii Duméril, 1853, p. 169 [holotype, M.N.H.N. No. 767 (two syntypes) from "Verapaz," Guatemala; Arthur Morelet collector; type locality restricted to Cobán, Alta Verapaz, Guatemala by Smith and Taylor (1950, p. 317)]. Brocchi, 1882, p. 31.

Hyla holochlora Salvin, 1860, p. 460, pl. 32, fig. 5 [holotype, B.M.N.H. No. 1947.2.24.23 from Cobán, Alta Verapaz, Guatemala; Osbert Salvin collector].

Agalychnis moreletii: Cope, 1865a, p. 110 [transfer of *Hyla moreletii* Duméril to *Agalychnis* Cope, 1865a]. Boulenger, 1882a, p. 422 [synonymized *Hyla holochlora* Salvin, 1860, with *Agalychnis moreletii* (Duméril, 1853)]. Günther, 1901 (1885-1902), p. 289 [part, specimens from Guatemala]. Smith and Taylor, 1948, p. 71. Duellman, 1968b, p. 4.

Phyllomedusa moreletii: Kellogg, 1932, p. 146 [transfer of *Agalychnis moreletii* (Duméril) to *Phyllomedusa* Wagler, 1830]. Funkhouser, 1957, p. 40. Stuart, 1963, p. 38.

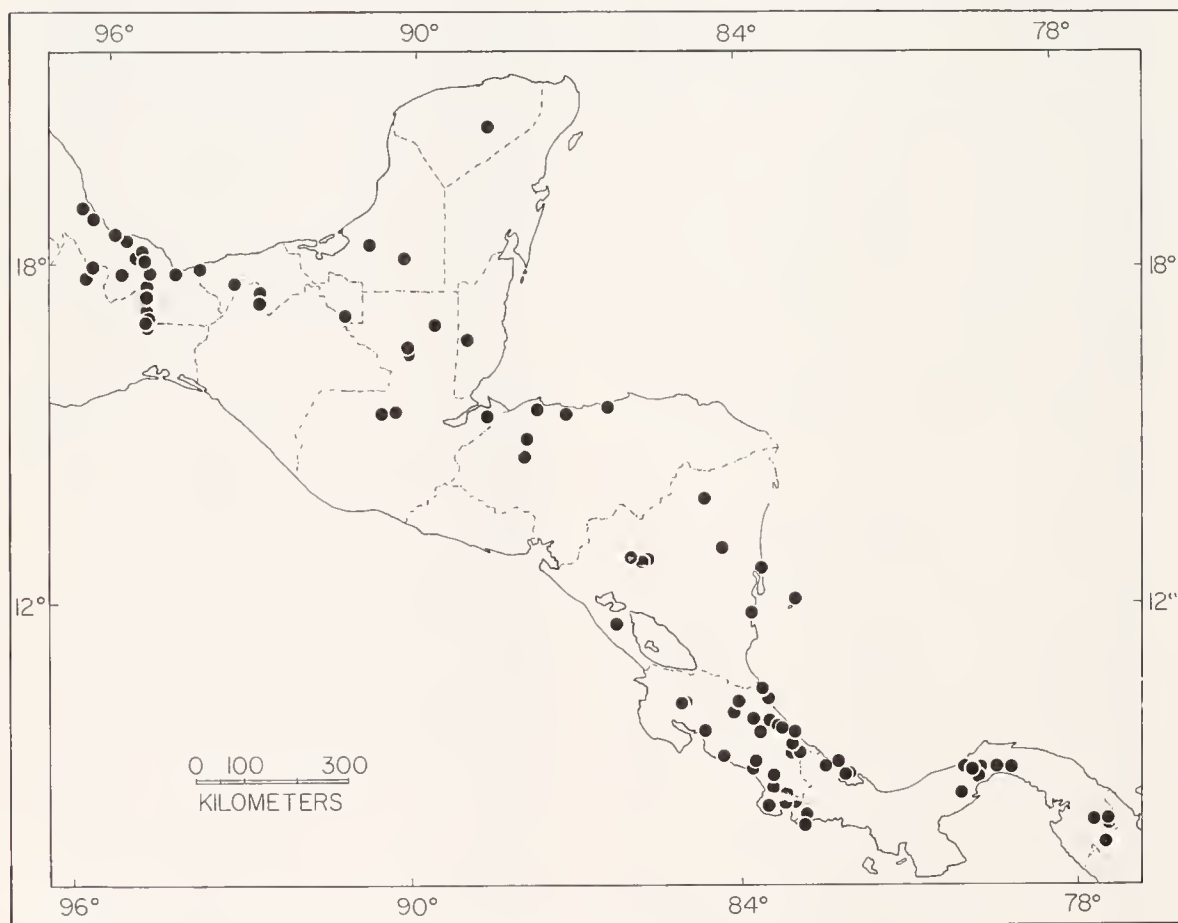


FIG. 37. Distribution of *Agalychnis callidryas*.

DIAGNOSIS: This moderate-sized species, having the hands and feet about three-fourths webbed, is distinguished from other species of *Agalychnis* by having uniformly orange flanks and thighs and a dark red eye. Some *Agalychnis callidryas* have orange thighs, but that species has blue, purple, or brown flanks with vertical cream-colored bars; *spurrelli* has yellow flanks and thighs, but differs in having black-bordered white spots on the dorsum and fully webbed hands and feet. Structurally *moreletii* is close to *annae*, which has uniformly blue flanks and thighs, an orange eye, slightly less webbing (figs. 28 and 30), and a smaller tympanum; the ratio of the diameter of the tympanum to that of the eye in *annae* is 0.431 to 0.627 (mean, 0.563), as compared with 0.603 to 0.714 (mean, 0.670) in *moreletii*.

DESCRIPTION: *Agalychnis moreletii* is a moderately large, slender species; males attain a maximum snout-vent length of 65.7 mm. (mean, 25 specimens, 60.6 mm.), and females reach 82.9 mm. (mean, six specimens, 78.3 mm.). In a sample of 25 males from Finca Chicoyou, Alta Verapaz, Guatemala, the ratio of tibia length to snout-vent length is 0.332 to 0.390 (mean, 0.367); the ratio of foot length to snout-vent length is 0.332 to 0.390 (mean, 0.367); the ratio of head length to snout-vent length is 0.311 to 0.344 (mean, 0.328); the ratio of head width to snout-vent length is 0.295 to 0.330 (mean, 0.309), and the ratio of the diameter of the tympanum to that of the eye is 0.603 to 0.714 (mean, 0.670). The frogs from Valentin, British Honduras, are slightly smaller, but the proportions are about the same. Eleven breeding males have snout-vent lengths of 51.1 to 59.0 (mean, 57.6) mm., and three females, 71.0 to 73.0 (mean, 72.4).

The head is about as wide as the body, and the top of the head is slightly convex. In dorsal profile the snout is narrow and acuminate. In lateral profile, in males, the snout gently slopes from the eyes to the nostrils and is further inclined to the tip of the snout; in females, the snout anterior to the nostrils is bluntly rounded. The nostrils are slightly protuberant and are about two-thirds the distance from the eyes to the tip of the snout. The canthus is rounded, but distinct; the loreal region is barely concave, and the lips are thin and slightly flared. A dermal

fold extending from the posterior corner of the eye to a point just posterior to the angle of the jaw conceals the upper and posterior edges of the tympanum, which otherwise is distinct. The tympanum is posterior, and slightly ventral to the eye and separated from it by a distance equal to about one-third of the diameter of the tympanum.

The upper arm is slender, whereas the forearm is robust. A narrow dermal fold extends from the elbow along the ventrolateral edge of the forearm and fourth finger to the disc. The fingers are relatively short and have large discs; the diameter of the disc on the third toe is greater than the diameter of the tympanum but less than that of the eye. The subarticular tubercles are moderately small and round, except that in many specimens the distal subarticular tubercles on the third and fourth fingers are bifid. The pollex is slightly enlarged in breeding males and bears a non-spinous horny nuptial excrescence. The fingers are about three-fourths webbed (fig. 28A). The webbing includes the basal phalanges to the base of the penultimate phalanx of the first and medial edges of the second and third fingers, to the middle of the penultimate phalanx on the fourth and lateral edge of the third finger, and to the base of the disc on the lateral edge of the second finger. The hind limbs are slender; the adpressed heels broadly overlap, and the tibio-tarsal articulation extends to the eye. A dermal fold extends along the median edge of the shank, across the heel, and along the ventrolateral edge of the tarsus to the disc on the fifth toe. In most specimens, a well-developed tarsal fold extends the full length of the tarsus, but in some individuals the fold is weak, especially distally. The inner metatarsal tubercle is large, flat, and elliptical. The toes are relatively short and slender, and the terminal discs are nearly as large as those on the hand. The subarticular tubercles are moderately large and round. The toes are about three-fourths webbed (fig. 30A). The web connects the first and second toes at the bases of the penultimate phalanges, extends from the base of the disc on the second toe to the base of the penultimate phalanx of the third toe, from the base of the disc of the third toe to the base of the penultimate pha-

lance of the fourth and on to the base of the disc of the fifth toe.

The anal sheath is long and folded laterally. The anal opening is directed ventrally at the level of the ventral surfaces of the thighs. The skin of the dorsum, chin, and ventral surfaces of the limbs, except the thighs, is smooth, whereas the skin on the belly and ventral surfaces of the thighs is moderately granular. The tongue is only slightly longer than wide, shallowly notched anteriorly, deeply notched posteriorly, and free behind for about one-third of its length. The denticulate processes of the prevomers are transverse ridges between the posterior margins of the ovoid choanae. Males have five to seven teeth on each process and a total of 10 to 13 (mean, 11.2) prevomerine teeth. Females have six to eight teeth on each process and a total of 12 to 16 (mean, 14.2) prevomerine teeth. The vocal slits are short; each is situated along a line from the posterolateral edge of the tongue to the angle of the jaw. The vocal sac is single, median, subgular, and not noticeably distensible.

The general coloration consists of a green dorsum, creamy yellow venter, and orange flank marks (pl. 43, fig. 1). The dorsal surfaces of the head, body, and hind limbs, forearms, fourth fingers, and fifth toes are leaf green, varying in some individuals to dark green and to pale green in others. The flanks, anterior and posterior surfaces of the thighs, the inner surfaces of the shanks, tarsi, and forearms, the upper arms, first three fingers and first four toes are orange. A broad diffuse creamy yellow stripe on the flanks separates the green dorsum from the orange flanks. The throat and belly are creamy yellow. The stripes on the outer edges of the forearm and tarsi are white. The iris is a dull red or maroon. The palpebral membrane is reticulated with gold, and the nuptial excrescences in breeding males are dark grayish brown.

Many individuals when active at night are dull green above; in these individuals the flank colors are dark orange. Recently metamorphosed young were pale green with creamy white flanks and thighs when found at night. By day the dorsum changed to a pale orange-brown.

In preservative, the dorsal surfaces of the

body, forearms, hind legs, fourth fingers, and fifth toes became dull dark blue. The rest of the surfaces are creamy white. In most individuals green is present only distally on the dorsal surfaces of the thighs, but in some specimens the green extends to the midlength of the thigh or even to the groin. Specimens from British Honduras are distinctive in having scattered white flecks on the dorsum.

TADPOLES: Ten hatchling tadpoles (stage 23) from Finca Chicoyou, Alta Verapaz, Guatemala, have body lengths of 5.8 to 6.8 (mean, 6.4) mm. and total lengths of 12.7 to 13.4 (mean, 13.0) mm. Five tadpoles in stages 30 to 31 from the same locality have body lengths of 16.5 to 18.5 (mean, 17.7) mm. and total lengths of 32.5 to 40.0 (mean, 46.1) mm., and one tadpole with hind limbs (stage 40) has a body length of 22.0 mm. and a total length of 55.0 mm.

Tadpoles are available in stages 28 to 36 with the mouth parts fully developed; these tadpoles have limb buds in the later stages (fig. 31E). In these tadpoles the body is noticeably deeper than broad; it is deepest posteriorly and widest at the level of the eyes. The snout in dorsal profile is truncate; in lateral profile it is acuminate, protruding, and dorsal to the midline. The nostrils are dorsolateral, about one-third the distance from the snout to the eyes, and directed anterolaterally. The eyes are dorsolateral and are directed laterally. The diameter of the eye equals about one-fifth of the greatest depth of the body. The spiracle is ventral and sinistral to the midline; the spiracular opening is at a point just posterior to the eye. The mouth is on the anteroventral surface of the protruding snout and directed anteriorly. The cloacal tube is short and dextral to the caudal fin. The caudal musculature is moderately robust; its depth at midlength of the tail is equal to the depth of the dorsal fin. Distally the caudal musculature is slender; it does not extend to the tip of the tail. The dorsal fin is deepest at midlength of the tail and does not extend onto the body. The ventral fin is slightly deeper than the dorsal fin and has equal depth on the anterior three-fourths of the tail.

The mouth has a shallow lateral fold. The median part of the upper lip is bare; the rest of the mouth is bordered by two rows of

papillae, except just lateral to the median bare part of the upper lip and the median part of the lower lip where but one row of papillae is present. Laterally scattered small papillae lie medially to the fringing rows. The upper beak is moderately deep and forms a broad arch; the lateral processes are slender, but expanded distally. The lower beak is moderately heavy. Both beaks have short, pointed serrations. There are two upper and three lower rows of teeth. The two upper rows are about equal in length and extend nearly to the papillae; the second upper row is interrupted medially. The first lower row is narrowly interrupted medially and equal in length to the upper rows; the second and third lower rows are successively shorter than the first.

The snout and top of the head and body are bluish gray with an olive-gray suffusion; in late stages the entire dorsal surfaces are olive-gray, but the sides of the body remain bluish gray. The ventral surfaces are silvery white. The caudal musculature is pale grayish tan. The caudal fins are transparent; scattered gray flecks are present on the fins and musculature. The iris is pale gold.

MATING CALL: The call of *Agalychnis moreletii* consists of a single "wor-or-orp," repeated at intervals of one to several minutes. The duration of the notes is from 0.09 to 0.27 (mean, 0.13) of a second. The notes are characterized by a pulse rate of 55 to 61 (mean, 58) pulses per second; each note consists of three to six (mean, 4.1) pulses, the last of which is greatly emphasized in intensity. The notes are poorly modulated and have as many as seven emphasized harmonics scattered throughout the frequency spectrum from about 1000 to 7500 cycles per second. The fundamental frequency falls between 160 and 185 (mean, 172) cycles per second, and the dominant frequency lies at 1110 to 1260 (mean, 1171) cycles per second (pl. 38, fig. 3).

NATURAL HISTORY: *Agalychnis moreletii* inhabits humid, usually montane, forests where it usually breeds in woodland pools. A large breeding congregation was found at a deep pool in a cloud forest at Finca Chicoyou, Alta Verapaz, Guatemala, on July 18, 1960. The presence of tadpoles in advanced stages,

as well as recently deposited eggs showed that the breeding activity there was spread over several weeks, if not months. Stuart (1948b) noted the presence of breeding adults and tadpoles in various stages of development in a temporary pond at Finca Samac, Alta Verapaz, on June 30, 1938. Taylor and Smith (1945) reported the species breeding on May 8, 1940, at Finca Juárez, Chiapas, México; the frogs were congregated around a pool in a stream, where eggs were deposited on boulders and on overhanging vegetation. Pyburn (1966) noted breeding *Agalychnis moreletii* near Sontecomapan, Veracruz, México, on August 11, 1962.

Eggs were found attached to every conceivable vegetative structure above the pond. One clutch was adherent to a small rotting stem projecting upward from a partially submerged log; another was attached to a vine between two bushes. Most clutches were attached to leaves of bushes and low trees to heights of about two meters, but one clutch was seen on a leaf of a branch approximately 12 meters above the pond. Nineteen clutches contained 23 to 77 (mean, 49) eggs. One clutch of 94 eggs seems to have resulted from two depositions, and another of 103 eggs looked as though it was the result of two or three depositions. In each of these the clutches did not appear uniform and eggs in different parts of the gelatinous masses were in different stages of development. The jelly is clear. In early stages of development, the yolk is pale green; in later stages it is creamy tan.

Small tadpoles, up to and including stage 31, were found amongst the leaf litter at the edge of the pool, whereas the larger tadpoles were observed in deep, open water in the middle of the pool. There they oriented themselves close to the surface nearly vertically with the head up. When disturbed they dove to greater depths.

One recently metamorphosed young has a snout-vent length of 19.8 mm.; only a vestigial web is present on the hand, and the toes are less than one-half webbed.

REMARKS: In the humid lower montane forests, or cloud forests, of southern México and northern Central America, *Agalychnis moreletii* is the ecological equivalent of *A.*

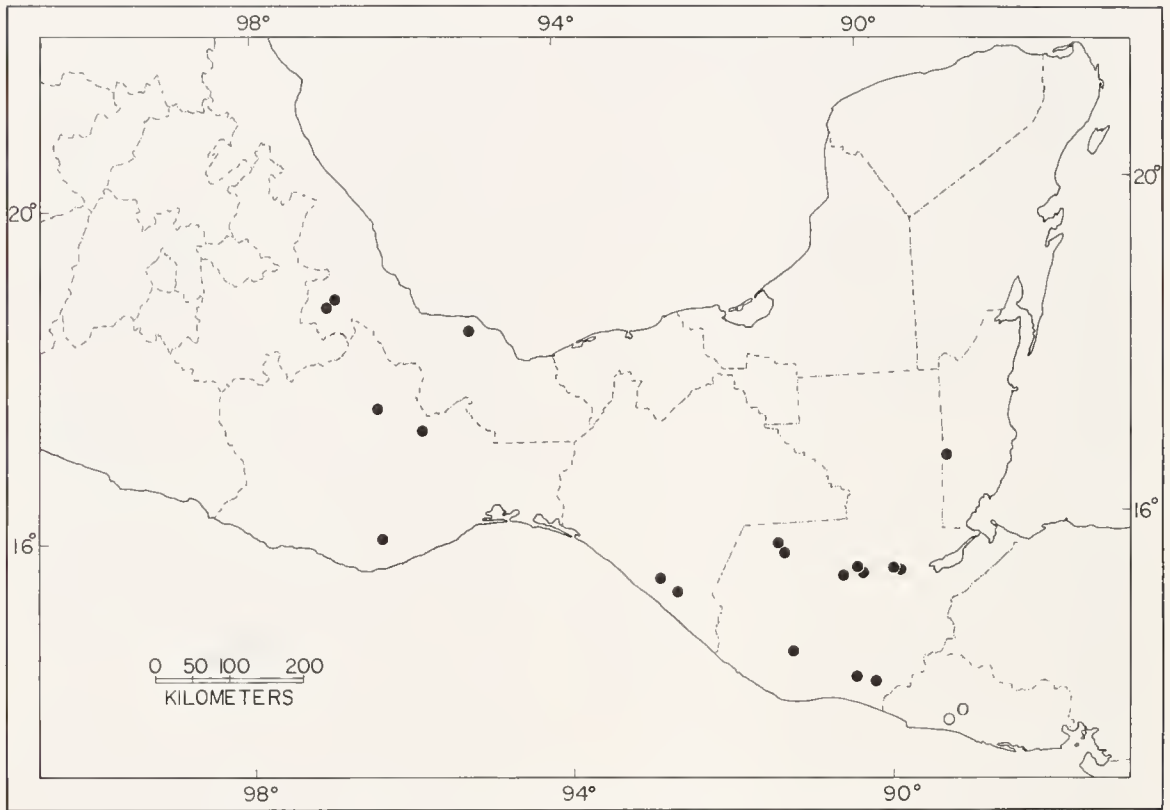


FIG. 38. Distribution of *Agalychnis moreletii*. Open circles are literature records.

annae, which occurs in the mountains of Costa Rica. Earlier workers, beginning with Boulenger (1882a) and including Funkhouser (1957), were not familiar with the animals in life and therefore were not aware of the striking differences in coloration between the northern Central American and Costa Rican populations that were pointed out by Duellman (1963d).

ETYMOLOGY: The specific name *moreletii* is a patronym for Arthur Morelet, the collector of the type specimen.

DISTRIBUTION: The range of *Agalychnis moreletii* is discontinuous in humid montane forests between about 500 and 1500 meters on the Atlantic slopes of Sierra Madre Oriental in Veracruz and Oaxaca, in the Sierra de los Tuxtlas in Veracruz, México, and in the mountains of Huehuetenango and Alta Vera-

paz in Guatemala. The species occurs at similar elevations on the Pacific slopes of Oaxaca and Chiapas, México, Guatemala, and El Salvador (fig. 38).⁴ The species also occurs at Valentin in British Honduras. Further collecting should reveal the presence of *Agalychnis moreletii* on the northern slopes of Chiapas and in the highlands of Honduras. In addition to the localities listed below, Mertens (1952b) recorded the species from the following localities in El Salvador: Finca Los Angeles and Finca El Paraiso, Departamento La Libertad, and San Antonio, Departamento San Salvador.

See Appendix 1 for the locality records of the 258 specimens examined.

⁴ Dr. Kraig Adler obtained *Agalychnis moreletii* near San Andreas de la Cruz, Guerrero, in December, 1969.

Agalychnis annae (Duellman)

Agalychnis moreletii: Boulenger, 1882a, p. 422 [part, specimens from Costa Rica]. Günther, 1901 (1885-1902), p. 289 [part, specimens from Costa Rica]. Taylor, 1952c, p. 802. Funkhouser, 1957, p. 40 [part, specimens from Costa Rica].

Phyllomedusa annae Duellman, 1963d, p. 1 [holotype, K.U. No. 64020 from Tapantí, Cartago Province, Costa Rica, 1200 meters; Ann S. Duellman collector].

Agalychnis annae Duellman, 1968b, p. 4.

DIAGNOSIS: This moderately large species is distinguished from other members of the genus *Agalychnis* by having uniformly dark blue flanks and thighs and an orange eye. Other species having blue on the flanks either are much smaller or have vertical cream-colored bars on the flanks; thus, *saltator* is smaller and has less webbing, and *callidryas* has vertical cream-colored bars on the flanks. *Agalychnis moreletii* most closely approaches *annae* in morphological characters, but differs in having orange flanks and thighs, a dark red eye, slightly more webbing on hands and feet (figs. 28 and 30), and a slightly larger tympanum; the ratio of the diameter of the tympanum to that of the eye in *moreletii* is 0.603 to 0.714 (mean, 0.670), as compared with 0.431 to 0.627 (mean, 0.563) in *annae*. *Agalychnis spurrelli* and *litodryas* lack the blue color on the flanks and thighs, and have dark red eyes and much larger, fully webbed hands and feet. *Agalychnis calcarifer* and *craspedopus* have yellow flanks and thighs boldly barred with black and prominent dermal appendages on the heels.

DESCRIPTION: *Agalychnis annae* is a moderately large, slender species; males attain a maximum snout-vent length of 73.9 mm. (mean, 35 specimens, 67.8 mm.), and females reach 84.2 mm. (mean, five specimens, 82.9 mm.). In a sample of 35 males from Tapantí, Cartago Province, Costa Rica, the ratio of tibia length to snout-vent length is 0.418 to 0.478 (mean, 0.447); the ratio of foot length to snout-vent length is 0.341 to 0.404 (mean, 0.370); the ratio of head length to snout-vent length is 0.290 to 0.328 (mean, 0.313); the ratio of head width to snout-vent length is 0.274 to 0.309 (mean, 0.294), the ratio of the diameter of the tympanum to that of the eye is 0.431 to 0.627 (mean, 0.563).

The head is narrower than the body, and

the top of the head is slightly convex. In dorsal profile the snout is narrow and slightly acuminate. In lateral profile, in males, the snout gently slopes from the eyes to the nostrils and is further inclined to the tip of the snout; in females, the snout is relatively blunt. The nostrils are slightly protuberant and are situated at about two-thirds of the distance from the eyes to the tip of the snout. The canthus is rounded and indistinct; the loreal region is slightly concave, and the lips are thin and not flared. A heavy dermal fold extending from the posterior corner of the orbit to a point just posterior to the angle of the jaw conceals the upper and posterior edges of the tympanum, which otherwise is prominent. The tympanum is situated posteroventrally to the eye and separated from the eye by a distance equal to about one-half of the diameter of the tympanum.

The upper arm is slender, whereas the forearm is robust. A narrow dermal fold extends from the elbow along the ventrolateral edge of the forearm onto the base of the fourth finger. The fingers are relatively short and have large discs; the diameter of the disc on the third finger is equal to that of the tympanum. The subarticular tubercles are small and round; the distal subarticular tubercles on the third and fourth fingers are the largest and are bifid in some specimens. The pollex is moderately enlarged in males; in breeding individuals it bears a large, non-spinous, horny nuptial excrescence. The fingers are about two-thirds webbed (fig. 28B); the webbing includes the basal phalanges to the base of the penultimate phalanx of the first, second, fourth, and lateral edge of the third finger, but only to the middle of the antepenultimate phalanx on the medial side of the third finger. The hind limb is slender; the heels of the adpressed limbs broadly overlap, and the tibiotarsal articulation extends to the posterior corner of the eye. Two small tubercles are present on the heel, and a thin dermal fold extends from the heel along the ventrolateral edge of the tarsus to the fifth toe. A weak tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is large, flat, and elliptical. The toes are relatively slender, and the terminal discs are slightly smaller than those on the hand. The

subarticular tubercles are moderately large and round. The toes are about three-fourths webbed (fig. 30B); the webbing extends to the base of the penultimate phalanges of the first, second, and medial edge of third toes, to the base of the disc on the lateral edge of the third toe, to the middle of the antepenultimate phalanx of the fourth toe, and to the middle of the penultimate phalanx of the fifth toe.

The anal sheath is long, and the anal opening is directed ventrally at the level of the ventral surfaces of the thighs. The skin of the dorsum, chin, and ventral surfaces of the limbs, except the thighs, is smooth, whereas the skin on the belly and ventral surfaces of the thighs is moderately granular. The tongue is half again as long as wide, notched anteriorly and posteriorly, and barely free behind. The denticulous processes of the prevomers are transverse ridges between the elliptical choanae. Males have five to seven teeth on each process and a total of 10 to 14 (mean, 12.0) prevomerine teeth. Females have eight to 12 teeth on each process and a total of 17 to 23 (mean, 20.2) prevomerine teeth. The vocal slits are small; each is situated about one-half the distance from the posterolateral edge of the tongue to the angle of the jaw. The vocal sac is single, median, subgular, and not noticeably distensible.

The general coloration consists of a green dorsum, creamy yellow venter, and blue flash marks (pl. 43, fig. 3). The dorsal surfaces of the head, body, thighs, shanks, tarsi, and forearms are bright leaf green; the anal region is pale leaf green. The flanks, anterior and posterior surfaces of the thighs, dorsal surfaces of the third fingers (usually except discs), dorsal surfaces of discs of fourth fingers, dorsal surfaces of fourth toes and discs of fifth toes, and the web between the fourth and fifth toes are blue. The stripe along the tarsus from the heel to the tip of the fifth toe and the stripe along the ventrolateral edge of the forearm from the elbow to the fourth finger are bright creamy yellow. The proximal dorsal surfaces of the upper arms are pink or lavender; distally the dorsal surfaces are blue. The dorsal surfaces of the fourth fingers are green; except as previously noted, the rest of the dorsal surfaces of the fingers, toes, discs, and

webbing is deep orange. The ventral surfaces of the limbs, and the belly in some specimens, are pinkish orange; the throat, chest, and belly (in most specimens) are creamy yellow. The lower lip is creamy white. The iris varies from bright orange to yellowish orange with a copper-colored periphery and reticulations. The palpebral membrane is reticulated with greenish gold. The nuptial excrescences in breeding males are brownish black.

The only noticeable variation in individual coloration is a general darkening of color at night. This is especially evident in the green, which changes to a dark green, and in blue, which changes to dark blue, almost purple in some individuals. Recently metamorphosed young are green like the adults, except that the young lack the blue coloring on the flanks, thighs, and extremities. The dorsal color changes to reddish brown in preservative.

In preservative, the dorsal surfaces of the body, forearms, hind legs, fourth fingers, and fifth toes change to dull purple. The flanks, anterior and posterior surfaces of the thighs, lateral surfaces of the tarsi, dorsal surfaces of the fourth toes, median surfaces of the forearms, and dorsal surfaces of the third fingers are brown. All of the ventral surfaces and the dorsal surfaces of the first and second fingers and first, second, and third toes are creamy yellow.

TADPOLES: Ten hatchling tadpoles (stage 23) from Tapantí, Cartago Province, Costa Rica, have body lengths of 3.2 to 4.4 (mean, 3.9) mm. and total lengths of 9.8 to 12.9 (mean, 11.3) mm. Five tadpoles in stage 31 from the same locality have body lengths of 11.0 to 12.4 (mean, 11.5) mm. and total lengths of 32.0 to 35.5 (mean, 33.2) mm., and two tadpoles having hind limbs (stage 39) have body lengths of 17.5 and 19.0 mm. and total lengths of 45.7 and 48.0 mm. The change in the length of the tail relative to the length of the body is evident in the comparison of the average ratio of tail length to total length in the three samples listed above. In tadpoles in stage 23 the ratio is 0.498; in stage 31, 0.656; and in stage 39, 0.638. The tail increases in length at a more rapid rate than the body until the hind limbs are well developed; then with the onset of metamorphosis the tail begins to shrink.

Tadpoles in stages 27 to 36 have the mouth parts fully developed and have undergone no external changes except for the development of small hind limbs in the later stages (fig. 31D). In these tadpoles, the body is as wide as deep; it is widest at the level of the eyes. In lateral profile, the snout is rounded; in dorsal profile, it is truncate. The nostrils are dorsolateral, about one-third of the distance from the snout to the eyes, and directed anterolaterally. The eyes are dorsolateral and directed laterally; the diameter of the eye equals about one-third of the depth of the body. The spiracle is ventral and sinistral to the midline; the spiracular opening is at a point slightly more than one-third the distance from the snout to the posterior end of the body. The mouth is anteroventral and directed anteriorly. The cloacal tube is short and dextral to the caudal fin. The lateral line organs are arranged in a curved line between the nostril and the eye and continue posteriorly just median to the eye on the dorsolateral surface of the body and thence onto the side of the anterior one-half of the tail. A branch of the lateral line system extends ventrally just behind the eye, then curves anteriorly below the eye, and extends nearly to the snout. The caudal musculature is rather weak; its depth at midlength of the tail is about one-third of the depth of the tail. The musculature does not quite extend to the tip of the tail; distally the musculature is slender and curved dorsally. The dorsal fin is deepest at midlength of the tail and does not extend onto the body; the ventral fin is deepest anteriorly.

The mouth has a shallow lateral fold. The median part of the upper lip is bare; the rest of the mouth is bordered by two rows of papillae, but laterally scattered small papillae lie medially to the fringing row. The upper beak is deep and forms a broad arch; the lateral processes are slightly expanded distally. The lower beak is massive. Both beaks have short, moderately pointed serrations. There are two upper and three lower rows of teeth. The upper rows are about equal in length, and the second upper row is interrupted medially. The first and second lower rows are about as long as the upper rows; the first lower row is interrupted medially in

many specimens, and the second lower row is broadly interrupted medially in some specimens. The third lower row is much shorter than the others (fig. 32D).

The snout and top of the head and body are heavily pigmented, giving a grayish brown appearance. The sides of the body are bluish gray, and the venter is pale blue with a decided silvery cast. The caudal musculature is pale grayish brown. The caudal fins are transparent with brown flecks on the proximal edges of the anterior one-half of both the dorsal and ventral fins. During development the amount of pigmentation on the dorsal surface of the body and on the caudal musculature increases, whereas the amount of pigment in the caudal fins decreases. The iris is yellow.

MATING CALL: The call of *Agalychnis annae* consists of a single note, "wor-or-orp," repeated at intervals of 40 seconds to two minutes or longer. The duration of the notes is from 0.16 to 0.44 (mean, 0.31) of a second. The notes are characterized by a pulse rate of 38 to 50 (mean, 42) pulses per second; each note consists of six to 17 (mean, 11.5) pulses, the last of which is emphasized in intensity. The notes are poorly modulated with as many as eight emphasized harmonics scattered throughout the frequency spectrum from about 1000 to 8800 cycles per second. The fundamental frequency falls between 140 and 185 (mean, 161) cycles per second, and the dominant frequency lies at 1044 to 1295 (mean, 1165) cycles per second (pl. 39, fig. 1).

NATURAL HISTORY: *Agalychnis annae* inhabits humid lowland and montane forests where it breeds in woodland pools. Duellman (1963d) reported breeding activity at Tapantí, Cartago Province, Costa Rica, from April 19 through June 6, 1961. Calling males were found there on March 22, 1966, and the species has been heard calling throughout the month of August. Although breeding activity may be concentrated in the early part of the rainy season (April and May), males probably call throughout the rainy season, which usually lasts until December. Possibly some breeding takes place throughout the rainy season.

The eggs are deposited in irregularly

shaped masses of jelly on leaves, branches, or vines from 35 to 240 cm. above the water (pl. 8, fig. 4). Sixteen clutches contained from 47 to 162 (mean, 106) eggs. The jelly is clear, and the individual egg membranes are visible. In early stages of development the yolk is pale green; in later stages the yolk is creamy tan. Measurements of 10 eggs in stage 4 of development (four cells) show that the diameter of the embryo is 3.36 to 3.44 (mean, 3.41) mm., the fertilization (vitelline) membrane is 3.51 to 3.65 (mean, 3.59) mm., and the outer envelope is 3.93 to 4.26 (mean, 4.12) mm. The eggs apparently hatch in about six days after deposition. One clutch of eggs in stage 4 of development found at La Palma, San José Province, Costa Rica on May 8 hatched on May 13. Hatching is accomplished by vigorous wriggling of the tadpole through the egg capsule. Some tadpoles adhere to the surface of the egg mass; by vigorous tail-flipping they free themselves and drop into the water. Other tadpoles were observed to break through the membranes and to slide down the egg mass and drop into the water.

Hatchling tadpoles sink to the bottom of the pond and remain motionless for several minutes before making faint swimming movements and sinking to the bottom again. At Tapantí, Cartago Province, Costa Rica, tadpoles in various stages of development to stage 36 were observed in a spring-fed pool partly filled with aquatic vegetation. Small tadpoles (up to stage 31) most frequently were found in vegetation-choked parts of the pond, whereas larger tadpoles were most often observed in deeper, open water. The large tadpoles orient themselves with their heads up and bodies at about a 45 degree angle to the surface of the water. The tip of the tail is curved slightly upwards and is fluttering continuously. The large tadpoles are extremely wary; upon the slightest disturbance they swim downward or into dense vegetation.

Tadpoles raised from eggs in the laboratory metamorphosed in 247 days. Probably development is more rapid under natural conditions. This suggestion is supported by Pyburn's (1963) report of metamorphosing *Agalychnis callidryas* in 79 days after hatching. Four metamorphosing young of *A. annae* have snout-vent lengths of 20.7 to 22.8 (mean, 21.7)

mm. In recently metamorphosed young, the head is proportionately larger than in the adults; the average ratio of head length to snout-vent length for the four young is 0.381, and the average ratio of head width to snout-vent length is 0.392. (Compare with proportions of adults given in preceding description.) The juveniles also differ from adults by having only about one-half as much webbing on the hands and feet.

REMARKS: This species was recorded from Costa Rica as early as 1882 by Boulenger, who together with succeeding workers through Taylor (1952c) and Funkhouser (1957) considered the Costa Rican frogs to be conspecific with *Agalychnis moreletii* in México and Guatemala. As pointed out by Duellman (1963d), knowledge of the Costa Rican and Guatemalan animals in life provided evidence that the two populations were not conspecific.

ETYMOLOGY: The specific name *annae* is a patronym for Ann S. Duellman.

DISTRIBUTION: *Agalychnis annae* occurs from low to moderate elevations (up to 1600 meters) on the Caribbean slopes of the Cordillera del Guanacaste, Cordillera Central, and Cordillera de Talamanca in Costa Rica (fig. 39). It probably occurs on the Caribbean slopes of western Panamá. One specimen (M.C.Z. No. 8031) purportedly from Esparta on the subhumid Pacific lowlands of Costa Rica, probably bears erroneous locality data.

See Appendix 1 for the locality records of the 239 specimens examined.

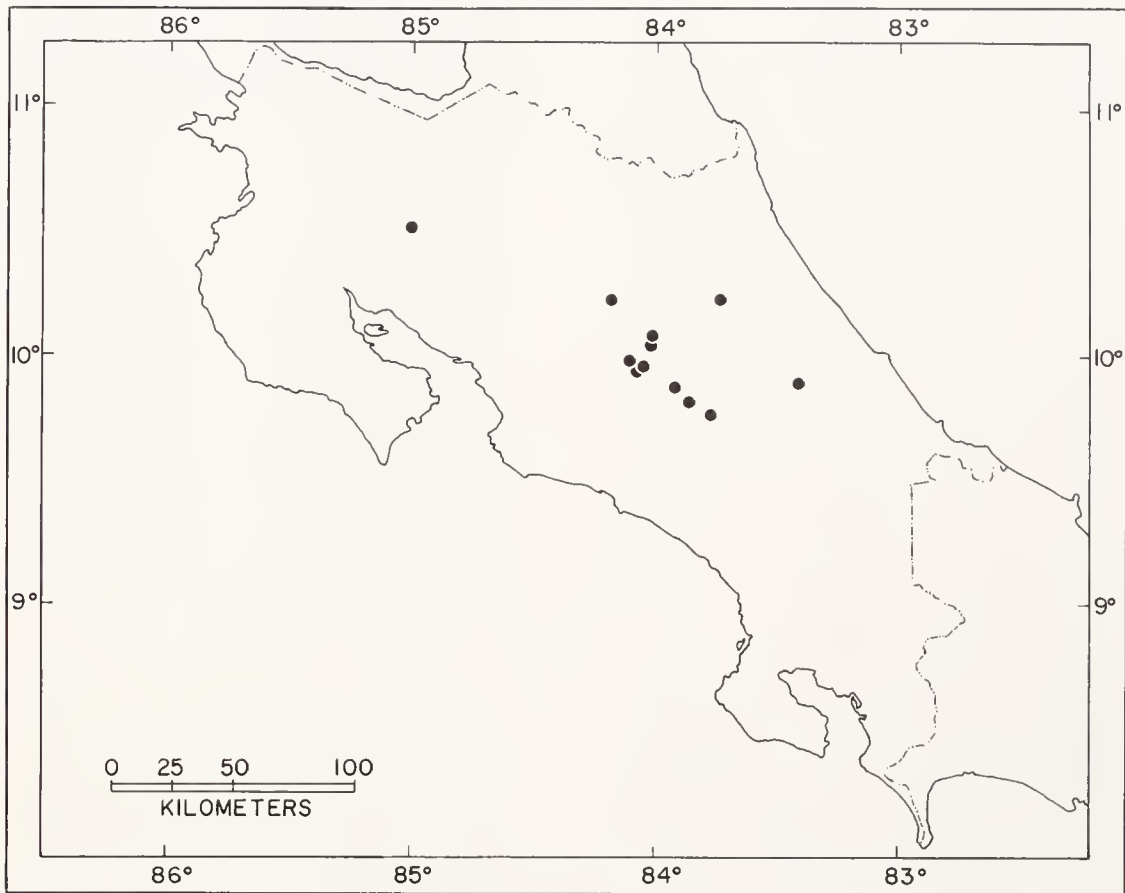
Agalychnis calcarifer Boulenger

Agalychnis calcarifer Boulenger, 1902a, p. 52 [holotype, B.M.N.H. No. 1947.2.24.22 from "Río Durango, northwestern Ecuador, 350 feet" (=Esmeraldas Province), Rosenberg collector]. Duellman, 1968b, p. 4.

Phyllomedusa (*Agalychnis*) *calcarifer*: B. Lutz, 1950b, p. 619, 620 [transfer of *Agalychnis calcarifer* Boulenger, 1902a to *Phyllomedusa* Wagler, 1830, at subgeneric status].

Phyllomedusa calcarifer: Funkhouser, 1957, p. 24 [transfer of *Agalychnis calcarifer* Boulenger, 1902a, to *Phyllomedusa* Wagler, 1830].

DIAGNOSIS: This moderate-sized *Agalychnis* is readily distinguished from all other members of the genus (except *craspedopus*) by having a large dermal flap on the heel, orange-yellow flanks and thighs with bold, black vertical bars, yellow eye, and an un-

FIG. 39. Distribution of *Agalychnis annae*.

marked palpebrum. In other species having orange or yellow flanks (*moreletii* and *spurrelli*, respectively), vertical black bars are absent. The only other known species of *Agalychnis* having vertical dark markings on the flanks and thighs is *craspedopus*, which differs from *calcarifer* by having large dermal flaps on the foot, dermal folds on the outer edges of the forearm and the fifth toe, and a truncate, instead of sloping, snout.

DESCRIPTION: *Agalychnis calcarifer* is a moderate-sized species; males attain a maximum snout-vent length of 64.0 mm. (mean, five specimens, 52.0 mm.), and females reach 78.5 mm. (mean, four specimens, 65.0 mm.). Two breeding males from Laguna, Darién Province, Panamá, have the following proportions: ratio of tibia length to snout-vent length, 0.515 and 0.520; ratio of foot length

to snout-vent length, 0.373 and 0.377; ratio of head length to snout-vent length, 0.323 in both; ratio of head width to snout-vent length, 0.333 and 0.335, and the ratio of the diameter of the tympanum to that of the eye, 0.760 and 0.775. One female from the same locality has a snout-vent length of 61.6 mm. and differs noticeably in proportions only by having a slightly larger tympanum (tympanum/eye is 0.816). The largest female (U.S.C. No. 496) is from Finca La Selva, Heredia Province, Costa Rica; it has a snout-vent length of 78.5 mm. and differs from the Panamanian specimens in having a relatively long foot (the ratio of foot length to snout-vent length is 0.411) and much larger tympanum (tympanum/eye ratio is 0.965).

The head is wider than the body, and the top of the head is barely convex. In dorsal

profile, the snout is rounded and terminally truncate. In lateral profile the snout slopes from the eyes to the nostrils and is sharply inclined to the tip of the snout in both sexes. The nostrils are slightly protuberant and are about three-quarters of the distance from the eyes to the tip of the snout. The canthus is heavy, rounded, and barely distinct; the loreal region is concave, and the lips are thin and not flared. A dermal fold extends from the posterior corner of the orbit along the upper and posterior edges of the tympanum to the angle of the jaw. The tympanum is distinct, posteroventral to the eye, and separated from the eye by a distance equal to about one-third of the diameter of the tympanum.

The upper arm is slender, whereas the forearm is moderately robust. A broad dermal fold extends from the elbow along the ventrolateral edge of the forearm to the disc on the fourth finger. The fingers are relatively short and have large discs; the diameter of the disc on the third finger is equal to, or slightly larger than, that of the tympanum. The subarticular tubercles are moderately large and round. One large female (U.S.C. No. 496) has bifid tubercles on the second, third, and fourth fingers; the other specimens have simple subarticular tubercles. The pollex is moderately enlarged and in breeding males it bears a large nuptial excrescence composed of many small horny spines. The fingers are about three-fourths webbed (fig. 27C). The web extends from the middle of the penultimate phalanx of the first finger to the base of the penultimate phalanx of the second finger, and from the base of the disc of the second finger to the base of the penultimate phalanx of the third. The web continues from the middle of the lateral edge of the penultimate phalanx of the third finger to the base of the disc on the fourth finger. The hind limb is slender; when the limbs are adpressed the heels overlap by about one-third the length of the thigh. The tibiotarsal articulation extends to a point between the eye and the tip of the snout in all specimens except the large female from Finca La Selva, Heredia Province, Costa Rica (U.S.C. No. 496), in which the heel extends anteriorly beyond the snout. A large, triangular dermal flap is present on the heel. From the edge of

the flap a narrow dermal fold extends along the outer edge of the tarsus to the disc on the fifth toe. Another less conspicuous dermal ridge extends the length of the dorsal edge of the tarsus onto the base of the fifth toe. The tarsal fold is weak and present only on the distal one-third of the tarsus. The inner metatarsal tubercle is rounded in profile and a long ellipse in shape. The toes are not especially slender; nor are they robust. The discs are about three-fourths the size of those on the hands. The subarticular tubercles are rather small and round. The toes are about three-fourths webbed (fig. 29C). The webbing extends to the base of the discs on the first, fifth, and lateral edges of the second and third toes, to the middle of the penultimate phalanx on the medial edge of the second toe, and to the base of the penultimate phalanges on the fourth and medial edge of the third toe.

The anal sheath is long and heavily folded laterally. The anal opening is directed posteroventrally at the median level of the thighs. The skin of the dorsum, chin, and ventral surfaces of the limbs, except the thighs, is smooth, whereas the skin on the belly and on the proximal posteroventral surfaces of the thighs is granular. The skin on the chest is smooth in all specimens, except the largest female (U.S.C. No. 496), which has tubercles on the chest. The tongue is half again as long as wide, notched anteriorly and posteriorly, and barely free behind. The dentigerous processes of the prevomers are transverse ridges between the choanae. Males have four or five teeth on each process and a total of nine or 10 (mean, 9.5) prevomerine teeth. One female has a total of 11 prevomerine teeth. The vocal slits are small apertures, one lying on each side of the posterior part of the attachment of the tongue. The vocal sac is single, median, subgular, and apparently not noticeably distensible.

The general coloration consists of a dark green dorsum with flanks and thighs orange marked with black bars (pl. 42, fig. 3). The dorsal surfaces of the body, forearms, shanks, tarsi, fourth fingers, and fifth toes are dark green. The flanks, narrow dorsal surfaces of upper arms and thighs, and throat are yellow. The belly, ventral surfaces of the limbs, hands,

feet, anterior and posterior surfaces of the thighs, inner surfaces of the shanks, tarsi, and forearms, and all but dorsal surfaces of upper arms are deep orange. The vertical bars on the flanks and transverse bars on the dorsal surfaces of the thighs and the inner surfaces of the forearms, shanks, and tarsi are black. The stripes on the outer edge of the forearm and fourth finger, on the inner edge of the shank and outer edge of the tarsus and fifth toe are yellow. A yellow stripe is present on the sides and across the posterior edge of the anal sheath. The edge of the lower lip is dark green. The iris is pale grayish lavender medially and dull yellow peripherally. The palpebral membrane is clear. The nuptial excrescences in breeding males are dark brown.

In preservative the dorsal surfaces of the body, forearms, shanks, and tarsi fade to dark blue. The black bars on the flanks and limbs remain black or change to dark brown. The orange and yellow fades to a pale creamy white.

In the small sample available for study, some variation in color pattern is evident. The number of black bars on the flanks varies from three to six and on the thighs from three to five. A juvenile (A.N.S.P. No. 23219) from Barro Colorado Island, Canal Zone, has a snout-vent length of 27.5 mm. and lacks black marks on the flanks and thighs. In the five adults examined from Panamá a narrow streak of green is present distally on the dorsal surface of the thighs. In these specimens, the green streak extends no farther than the mid-length of the thigh, but in one specimen from Costa Rica and one described from Colombia by Boulenger (1913) the streak extends the length of the thigh. Boulenger (1913, p. 1023) described the colors in life of the specimen from Peña Lisa, Condoto, Chocó, Colombia, (based on field notes taken by Dr. H. Spurrell) as follows: "... brilliant sage-green above, flanks and upper surface of thighs (with the exception of a narrow green streak) rich orange-yellow with black bars; hands and feet and lower parts orange-yellow; iris grey, bordered with orange-yellow; lower eyelid transparent, edged with "turquoise-blue."

TADPOLES: The tadpoles of *Agalychnis calcarifer* are unknown. Eggs, presumably of

this species, were found on a dead leaf over a pool of water in a log. Thus, it may be assumed that the tadpoles of this species, like those that are known in the genus, develop in quiet water.

MATING CALL: No recordings of the call are in existence; to my knowledge no biologist has heard the species.

NATURAL HISTORY: Little is known about this frog, which is represented in museum collections by only nine specimens. Most of the individuals were found sitting on vegetation in forests at night. At Laguna, Darién Province, Panamá, on July 19, 1963, two males in breeding condition and one spent female were found by day. The frogs were hidden beneath parts of a log overhanging a pool of water that had collected in the log. A clutch of eggs was adhering to a dead leaf hanging over the pool. The 16 eggs were encased in clear jelly; the outer envelopes were not evident. The eggs were in the yolk-plug stage. The average diameter of the eggs is 3.5 mm. and of the vitelline membrane, 4.0 mm.

REMARKS: The presence of the triangular dermal flap on the heel, extensive webbing, and black bars on the flanks and thighs sets *Agalychnis calcarifer* apart from all other Central American species in the genus. However, *calcarifer* seems to be closely related to *Agalychnis craspedopus* (Funkhouser). The latter is known from only two specimens from Chicherote, Napo Province in eastern Ecuador. *Agalychnis craspedopus* resembles *calcarifer* in general structure and color pattern, but differs by having a truncate snout, less webbing, and extensive dermal folds on the outer edge of the tarsus and fifth toe. These comparisons were made with the holotype of *craspedopus* (S.U. No. 10310).

ETYMOLOGY: The specific name *calcarifer* alludes to the triangular dermal flap on the heel and is derived from the Latin *calcar* meaning a spur and *fero* meaning to carry.

DISTRIBUTION: *Agalychnis calcarifer* is known from three localities in Central America (fig. 40) and from two in South America [Río Durango, Esmeraldas, Ecuador (Boulenger, 1902a) and Peña Lisa, Condoto, Chocó, Colombia (Boulenger, 1913)]. All localities are in the humid tropical lowlands (highest elevation, 820 meters) on the Carib-

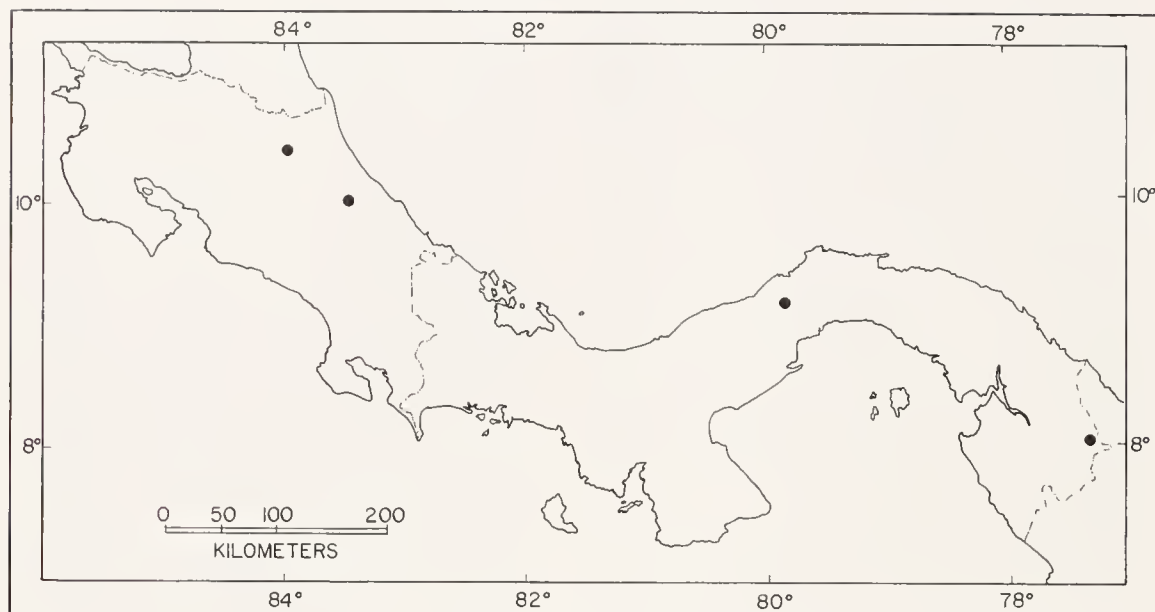


FIG. 40. Distribution of *Agalychnis calcarifer*.

bean side of Costa Rica and central Panama and on the Pacific side of eastern Panamá, Colombia, and Ecuador.

See Appendix I for the locality records of the nine specimens examined.

Agalychnis spurrelli Boulenger

Agalychnis spurrelli Boulenger, 1913, p. 1024, fig. 177, pl. 103 [holotype, B.M.N.H. Nos. 1947.2.24.24 and 25 (two syntypes) from Peña Lisa, Condoto, Chocó Province, Colombia; H. Spurrell collector]. Duellman, 1968b, p. 4.

Phyllomedusa spurrelli: Funkhouser, 1957, p. 39 [transfer of *Agalychnis spurrelli* Boulenger, 1913 to *Phyllomedusa* Wagler, 1830].

DIAGNOSIS: This medium to large species having fully webbed hands and feet can be distinguished from all other *Agalychnis* by the presence of bright yellow flanks and thighs, dark red eye, and dorsum usually marked with black-bordered white spots. Although *litodryas* is nearly identical with *spurrelli* in structural features, the former can be separated in that it lacks pigment on the flanks and thighs and has no white spots on the dorsum. White pustular spots occur on the dorsal surfaces of many species of *Agalychnis*, but only in *spurrelli* are these spots always narrowly outlined in black.

DESCRIPTION: Individuals in some popula-

tions of *Agalychnis spurrelli* attain a large size. The largest male examined is from Tacareuna, Darién Province, Panamá, and has a snout-vent length of 75.6 mm., whereas the largest recorded female is from Peña Lisa, Chocó, Colombia, and has a snout-vent length of 92.8 mm. (*vide* Cochran and Goin, 1970). In a sample of seven males from Barro Colorado Island, Canal Zone, Panamá, the ratio of tibia length to snout-vent length is 0.473 to 0.514 (mean, 0.499); the ratio of foot length to snout-vent length is 0.368 to 0.411 (mean, 0.382); the ratio of head length to snout-vent length is 0.296 to 0.330 (mean, 0.311); the ratio of head width to snout-vent length is 0.310 to 0.328 (mean, 0.315), and the ratio of the diameter of the tympanum to that of the eye is 0.535 to 0.622 (mean, 0.569).

The specimens from southeastern Costa Rica are much smaller than those from central and eastern Panamá (table 12) and have relatively smaller tympani. Cochran and Goin (1970) gave the range in snout-vent length of eight males from Río Manso, Córdoba, Colombia, as 47.2 to 52.2 mm. and of two females as 62.4 and 66.3 mm. These measurements are similar to those obtained from 14 males and four females from southeastern Costa Rica, which have snout-vent lengths

respectively of 48.2 to 56.4 (mean, 51.9) mm. and 60.2 to 71.8 (mean, 65.6) mm., whereas the snout-vent lengths of 15 males and three females from Panamá are much greater. The snout-vent length in males is 67.6 to 75.6 (mean, 72.1) mm. and in females, 81.6 to 86.7 (mean, 84.3) mm. Thus, on the basis of the small samples available the largest individuals apparently occur in the middle of the range, whereas individuals from the known peripheral areas are smaller, although the largest known specimen, a female, is from the southern end of the range in Colombia.

The head is wider than the body, except in gravid females, and the top of the head is flat. In dorsal profile, in both sexes the snout moderately slopes from the eyes to the nostrils and is further inclined to the tip of the snout. The nostrils are slightly protuberant and are about two-thirds of the distance from the eyes to the tip of the snout. The canthus is rounded, but distinct; the loreal region is slightly concave, and the lips are thin and moderately flared. A heavy dermal fold extending from the posterior corner of the orbit to a point just posterior to the angle of the jaw conceals the upper and posterior edges of the tympanum, which otherwise is prominent. The dermal fold continues posteriorly as a flap above the insertion of the arm to the axilla. The tympanum is situated posterior, and slightly ventral, to the eye and is separated from the eye by a distance slightly less than one-half the diameter of the tympanum.

The upper arm is slender, and the forearm is robust. A conspicuous dermal fold extends across the elbow and along the ventrolateral edge of the forearm to the disc on the fourth

finger. The fingers are relatively short and have large discs; the diameter of the disc on the third finger is about equal to the diameter of the eye in Panamanian specimens, but only equal to about two-thirds the diameter of the eye in Costa Rican specimens. The subarticular tubercles are round and moderate in size; in some large males and most females the distal subarticular tubercles on the third and fourth fingers are flattened and bifid. In one female (K.U. No. 77515) all, except the proximal tubercle on the fourth finger, are bifid. The pollex is greatly enlarged and bears a large, horny nuptial excrescence made up of minute spines. The fingers are about three-fourths webbed (fig. 28C). The web connects the first two toes at the bases of the penultimate phalanges, continues from the base of the disc of the second finger to the base of the penultimate phalanx of the third finger, and connects the third and fourth fingers at the bases of the discs. The hind limbs are slender. In Panamanian specimens, the heels of the adpressed limbs overlap by a distance equal to about one-third the length of the shank, and the tibiotarsal articulation extends to the anterior corner of the eye, whereas in Costa Rican specimens the heels barely overlap, and the tibiotarsal articulation extends to a point about midway between the eye and the tip of the snout. The skin on the shank tends to form a thin longitudinal fold on the ventrolateral and ventromedian surfaces. A thin dermal fold extends across the heel and along the outer edge of the tarsus to the base of the disc on the fifth toe. A relatively strong tarsal fold extends the full length of the tarsus. The inner metatarsal

TABLE 12
Comparison of Four Samples, with Means in Parentheses, of Adult Males of *Agalychnis spurrelli*.

Locality	N	Snout-vent Length (mm.)	Tibia Length/ S-V L	Foot Length/ S-V L	Tympanum/ S-V L
San Isidro el General, Costa Rica	10	49.9-56.4 (53.0)	0.457-0.493 (0.476)	0.365-0.413 (0.394)	0.508-0.647 (0.558)
Rincón de Osa, Costa Rica	4	48.2-49.9 (49.0)	0.502-0.528 (0.514)	0.381-0.420 (0.399)	0.545-0.574 (0.557)
Barro Colorado Island, Panamá	7	70.6-74.6 (72.9)	0.473-0.514 (0.499)	0.368-0.411 (0.382)	0.535-0.622 (0.569)
Tacarcuna, Panamá	8	67.6-75.6 (71.1)	0.495-0.520 (0.508)	0.386-0.413 (0.401)	0.462-0.676 (0.585)

tubercle is low, flat, and elliptical. The toes are long and slender, and the discs are slightly smaller than those on the fingers. The sub-articular tubercles are large and subconical. Supernumerary tubercles are present on the proximal segments of all of the toes. In Panamanian specimens, the toes are fully webbed (fig. 30C). Some males from Costa Rica have the web extending only to the bases of the penultimate phalanges on the fourth toe and the median edges of the second and third toes.

The anal sheath is long, and the anal opening is directed ventrally at the level of the ventral surfaces of the thighs. The skin of the dorsum, chin, and ventral surfaces of the limbs, except the proximal surfaces of the thighs is smooth, whereas that on the belly and proximal surfaces of the thighs is granular. The granules form a distinct row on the posteroventral surfaces of the thighs. The tongue is about twice as long as wide, notched anteriorly and posteriorly, and free behind for about one-third of its length. The dentigerous processes of the prevomers are transverse ridges between the narrowly elliptical choanae. Males have seven to nine teeth on each process and 14 to 17 (mean, 15.3) prevomerine teeth. Females have eight or nine teeth on each process and a total of 16 to 18 (mean, 17.0) prevomerine teeth. The vocal slits are short and are situated along the posteromedian edges of the rami. The vocal sac is single, median, subgular, and not noticeably distensible.

The general coloration consists of a green dorsum, usually with black-bordered white spots, and yellow flanks, thighs, and venter (pl. 43, fig. 6). Specimens from Barro Colorado Island, Canal Zone, Panamá (K.U. Nos. 77499-77506), are pale leaf green on the dorsal surfaces of the head, body, limbs, fourth fingers, and fourth and fifth toes. The chin and throat are yellow; all other ventral surfaces, flanks, anterior and posterior surfaces of the thighs, leading edges of tarsi, first four toes, upper arms, inner edges of forearms, first three fingers, and all webbing and discs are orange. In some individuals, a narrow dark olive-green line separates the orange flanks from the green dorsum. All individuals have black-bordered spots on the dorsum.

The stripes extending from the elbow along the outer edge of the forearm to the disc of the fourth finger, along the edge of the tarsus from the heel to the disc of the fifth toe, and across the anal flap are yellowish cream. The iris is deep crimson, and the palpebral membrane is reticulated with greenish gold. The nuptial excrescences in breeding males are dark brown.

Specimens from Tacarcuna, Darién Province, Panamá (K.U. Nos. 77507-77515), are like those from Barro Colorado Island, except that the throat and chest are creamy white instead of yellow. Notes on the coloration in life of 11 specimens from 16 kilometers southwest of San Isidro el General, San José Province, Costa Rica (U.S.C. No. 7220) provided by Dr. Jay M. Savage indicate that these specimens are colored like those from Barro Colorado Island, except that the throat and chest are cream, and the belly is pale orange. Savage's notes on a male (U.S.C. No. 7235) from the Península de Osa, Puntarenas Province, Costa Rica, indicate that in this specimen the dorsal white spots are narrowly outlined by dark green. All Panamanian specimens and, according to Cochran and Goin (1970), all Colombian specimens have conspicuous white spots, narrowly outlined by black, on the dorsum, but four of the 18 adult specimens from southeastern Costa Rica lack white spots.

In preservative the dorsal ground color is blue to purple, and the ventral surfaces, flanks, upper arms, anterior and posterior surfaces of thighs, and hands and feet are creamy white. The dorsal spots are white with black borders.

Metamorphosing young are green above and creamy white below.

TADPOLES: Ten tadpoles in stages 34 to 37 from Rincón de Osa, Puntarenas Province, Costa Rica, have body lengths of 14.5 to 17.0 (mean, 15.8) mm. and total lengths of 40.0 to 43.0 (mean, 41.5) mm. The ratio of tail length to total length is 0.575 to 0.654 (mean, 0.619). The largest tadpole in stage 41 has a body length of 19.5 mm., a total length of 52.3 mm.; the ratio of tail length to total length is 0.589.

Tadpoles in stage 36 have fully developed mouth parts and have undergone no external

changes except for the development of small hind limbs (fig. 31C). In these tadpoles the body is as wide as deep; it is nearly of uniform width posterior to the eyes. The top of the head is flat. In lateral profile the snout is rounded; in dorsal profile it is truncate. The nostrils are dorsolateral, and directed laterally; the diameter of the eye equals about one-third of the depth of the body. The spiracle is a flap-like tube ventral and sinistral to the midline; the spiracular opening is at a point about two-thirds of the distance from the snout to the posterior end of the body. The mouth is anteroventral and directed anteriorly. The cloacal tube is short and dextral to the caudal fin. The caudal musculature is rather weak; its depth at midlength of the tail is about one-third of the depth of the tail. The musculature extends nearly to the tip of the tail; distally the musculature is slender and curved dorsally. The dorsal fin is shallow anteriorly and does not extend onto the body; the ventral fin is deepest at about one-third of its length.

The mouth has a shallow lateral fold. The median two-thirds of the upper lip is bare; the rest of the mouth is bordered by two or three rows of papillae, and laterally additional papillae are present. The upper beak is moderately shallow and forms a broad arch; the lateral processes are barely expanded distally. The lower beak is heavy. Small blunt serrations are present on the upper beak and small pointed serrations on the lower beak. There are two upper and three lower rows of teeth. The upper rows are about equal in length, and the second upper row is interrupted medially. The lower rows are much shorter than the upper rows; the lower rows are progressively shorter, so that the third lower row is the shortest (fig. 32C).

The snout and top of the head are olive-brown; the sides of the body are dark bluish gray, and the venter is pale bluish gray. The caudal musculature is grayish tan. Dark brown flecks are present on the sides of the body and on the proximal edges of the anterior one-half of the fins; dark brown reticulations are present on the anterior one-half of the caudal musculature. During development the amount of dark pigment increases,

so that in tadpoles in stage 41, the entire tail is marked with bold reticulations.

MATING CALL: The call of *Agalychnis spurrelli* consists of a single, low-pitched groan repeated at intervals of 10 to 17 seconds. The duration of the notes is from 0.34 to 0.40 (mean, 0.37) of a second. The notes are characterized by a pulse rate of 60 to 90 (mean, 75) pulses per second. Each note consists of 19 to 24 (mean, 23.5) pulses; the last pulse is not intensified. The fundamental frequency varies from 87 to 100 (mean, 94) cycles per second, and the dominant frequency varies from 435 to 700 (mean, 568) cycles per second (pl. 39, fig. 2).

NATURAL HISTORY: *Agalychnis spurrelli* inhabits humid tropical lowland forests, where it breeds in woodland pools and water-filled cavities in logs. Calling males were found in trees above and near a water-filled cavity in a log on Barro Colorado Island, Canal Zone, on June 3, 1963, and males were calling from a large tree in a temporary pond at Tacarcuna, Darién Province, Panamá, on July 16, 1963. Boulenger (1913, p. 1024) reported that a clasping pair was obtained on April 2 at Peña Lisa, Condoto, Chocó, Colombia, and that 66 eggs were preserved with the specimens.

Dr. John D. Lynch obtained the tadpoles and metamorphosing young of this species at a locality 4.5 kilometers west of Rincón de Osa, Puntarenas Province, Costa Rica, on August 7 and 10, 1966. Tadpoles were found in a water-filled cavity in a log at the edge of the forest and in a shallow, weedy pond. The tadpoles orient themselves with their heads up and bodies at about a 45 degree angle to the surface of the water, but dive for cover at the slightest disturbance. By day when the pond was in direct sunlight the tadpoles were hidden among leaves on the bottom of the pond.

Three metamorphosing young have snout-vent lengths of 18.2 to 20.0 (mean, 19.1) mm. The head is proportionately larger than in the adults, and there is less webbing on the hands and feet. One individual has distinct white spots on the dorsum.

REMARKS: The number of known specimens is insufficient to interpret the great disparity in size between the populations in

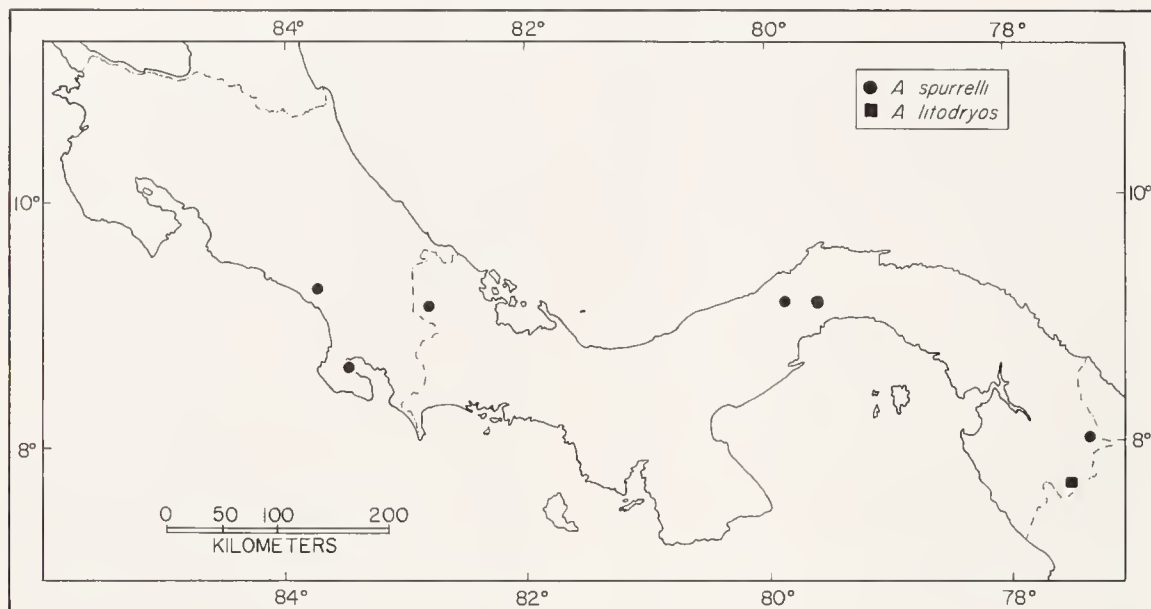


FIG. 41. Distribution of *Agalychnis spurrelli* and *Agalychnis litodryas*.

southeastern Costa Rica and those in central and eastern Panamá. Furthermore, life history data are lacking for the Panamanian populations, and recordings of the mating calls are not available for the Costa Rican populations.

ETYMOLOGY: The specific name *spurrelli* is a patronym for Dr. H. G. F. Spurrell, who collected the type series in Colombia.

DISTRIBUTION: *Agalychnis spurrelli* occurs at low elevations (up to 885 meters) in humid tropical forests in the Golfo Dulce region of southeastern Costa Rica, the Caribbean slopes of western Panamá, and the Pacific lowlands of eastern Panamá southward along the Pacific coast of Colombia (fig. 41).

See Appendix 1 for the locality records of the 47 specimens examined.

Agalychnis litodryas (Duellman and Trueb)

Phyllomedusa litodryas Duellman and Trueb, 1967, p. 125 [holotype, K.U. No. 96149 from approximately 1 kilometer west-southwest of the junction of the Río Mono and the Río Tuira, Darién Province, Panamá, elevation 130 meters; William E. Duellman collector].

Agalychnis litodryas: Duellman, 1968b, p. 4 [transfer of *Phyllomedusa litodryas* Duellman and Trueb, 1967, to *Agalychnis* Cope, 1864].

DIAGNOSIS: This large species having fully webbed hands and feet differs from other

Agalychnis by lacking pigment on the hands, feet, thighs, and flanks. Structurally it is most like *spurrelli*, which has bright yellow flanks, thighs, and extremities; furthermore, the dorsum is uniformly green in *litodryas*, whereas the dorsum in *spurrelli* is green with black-bordered white spots.

DESCRIPTION: Only the type specimen, an adult male, is known. This specimen has a snout-vent length of 70.2 mm. and the following proportions: tibia length/snout-vent length, 0.523; foot length/snout-vent length, 0.392; head length/snout-vent length, 0.345; head width/snout-vent length, 0.307, diameter of tympanum/diameter of eye, 0.705.

The head is as wide as the body, and the top of the head is flat. In dorsal profile the snout is acuminate. In lateral profile, the snout slopes from the eyes to the nostrils and is further inclined from the nostrils to the tip of the snout. The nostrils are protuberant laterally and are about two-thirds of the distance from the eyes to the tip of the snout. The canthus is rounded and distinct; the loreal region is slightly concave, and the lips are thin and moderately flared. A thin dermal fold extends from the posterior corner of the orbit, covering the dorsal and posterior edges of the tympanum, to a point just behind the angle of the jaw; from there it continues pos-

teriorly as a dermal flap to a point above the insertion of the arm. The tympanum is distinct, posteroventral to the eye, and separated from the eye by a distance equal to one-third of the diameter of the tympanum.

The upper arm is slender, and the forearm is robust. A narrow dermal fold extends from the elbow along the ventrolateral edge of the forearm and the fourth finger to the disc on the fourth finger. The fingers are short, and the discs are very large, all larger than the tympanum. The distal subarticular tubercles on the third and fourth fingers are large and round; the other subarticular tubercles are smaller and conical. The pollex is enlarged, has a flat, elliptical ventral surface, and bears a large, horny, non-spinous nuptial excrescence. The fingers are about three-fourths webbed (fig. 28D). The web extends to the base of the penultimate phalanx on the first finger and medial edges of the second and third fingers, and to the discs on the other fingers. The hind limbs are slender; when the limbs are adpressed the heels overlap by about one-third the length of the thighs. The tibiotarsal articulation extends to the nostril. There is no dermal fold along the outer edge of the tarsus, but a small dermal flap is present on the posteroventral surface of the heel. The tarsal fold is moderately strong and extends the full length of the tarsus. The inner metatarsal tubercle is large, flat, elliptical, and broadly visible from above. The toes are moderately long and slender. The discs are large, nearly as large as the tympanum. The subarticular tubercles are large and conical. Small supernumerary tubercles are present on the proximal segments of all toes, except the first. The toes are fully webbed; the web extends to the bases of the discs on all toes (fig. 30D).

The anal sheath is long, and the anal opening is directed ventrally at the level of the ventral surfaces of the thighs. The skin of the dorsum, chin, chest, and ventral surfaces of the limbs, except the thighs, is smooth, whereas the skin on the belly and ventral surfaces of the thighs is moderately granular. The granules form a distinct row on the posteroventral edge of the thigh. The tongue is twice as long as wide and deeply notched posteriorly. It is free posteriorly for about one-

third of its length. The dentigerous processes of the prevomers are narrow transverse elevations between the anterior margins of the small ovoid choanae. Ten teeth are present on each process. The vocal slits are small and lie along the posterior one-fourth of the rami of the jaws. The vocal sac is single, median, subgular, and not noticeably distensible.

The general coloration consists of a uniform green dorsum and unpigmented flanks and thighs (pl. 43, fig. 4). The dorsal surfaces of the head, body, forearm, thighs, shanks, tarsi, third and fourth fingers, and fourth and fifth toes are uniform pale green; the throat and belly are creamy white. A narrow yellowish white stripe extends along the inner edge of the shank, across the heel, and along the outer edge of the tarsus and fifth toe. A narrow yellowish white stripe is present on the outer edge of the forearm and fourth finger. The flanks, anterior and posterior surfaces of the thighs, inner surfaces of the tarsi, upper arms, inner surfaces of forearms, first and second fingers, first, second, and third toes, and webbing lack pigment, so that these surfaces appear pale pinkish gray. The iris is dark red, and the palpebral membrane is reticulated with gold. The nuptial excrescence is dark gray.

In preservative the dorsal surfaces of the body, forearms, hind limbs, fourth and fifth toes, and third and fourth fingers, are uniform bluish green. The chin, chest, and belly are white; other ventral surfaces are creamy gray. The lines on the forearm and hind limbs are white.

The one specimen that is known was confined in a cloth sack overnight; when it was first observed the following morning the dorsum had changed from pale green to a dark olive-green.

TADPOLES: The tadpoles of this species are unknown.

MATING CALL: The mating call consists of a single low-pitched "groan." In the one recording available the duration of the note is 0.15 of a second. The pulse rate is 105 pulses per second; the note has 16 pulses, and the last pulse is not intensified. The fundamental frequency is 104 cycles per second, and the dominant frequency is 1664 cycles per second (pl. 39, fig. 3).

NATURAL HISTORY: The only known specimen was found on a bush in a swamp at night. *Agalychnis callidryas* was breeding in the swamp, and individuals of *Phyllomedusa venusta* were present there.

REMARKS: Structurally, *Agalychnis litodryas* is strikingly similar to *A. spurrelli*, which has a slightly higher and less sloping snout, somewhat smaller discs, and more supernumerary tubercles. The most noticeable differences are in coloration; *A. spurrelli* has yellow flanks, thighs, hands, feet, and chin, whereas in *litodryas*, these structures lack pigment, except the chin which is white. Furthermore, *litodryas* lacks the black-bordered white spots on the dorsum that are always present on *spurrelli*.

ETYMOLOGY: The specific name alludes to the absence of flash-colors and is derived from the Greek *litos* meaning plain and the Greek *Dryas*, a tree nymph.

DISTRIBUTION: Currently this species is known only from eastern Darién Province, Panamá (fig. 41).

See Appendix 1 for the locality record of the one specimen examined.

Genus *Phyllomedusa* Wagler

Phyllomedusa Wagler, 1830, p. 201 [type species, *Rana bicolor* Boddaert, 1772, by original designation].

Pithecopus Cope, 1866b, p. 86 [type species, *Phyllomedusa azurea* Cope, 1862 (= *Phyllomedusa hypochondrialis* Daudin, 1803) by original designation].

Hylomantis Peters, 1872, p. 772 [type species *Hylomantis aspersa* Peters, 1872, by monotypy].

Phrynomedusa Miranda-Ribeiro, 1923, p. 3 [type species, *Phrynomedusa fimbriata* Miranda-Ribeiro, 1923, by subsequent designation (Funkhouser, 1957)].

Bradymedusa Miranda-Ribeiro, 1926, p. 104 [type species, *Bradymedusa moschada* Miranda-Ribeiro, 1926 (= *Phyllomedusa rohdei* Mertens, 1926), by subsequent designation (Funkhouser, 1957)].

GENEROTYPE: Wagler (1830, p. 201) proposed the generic name *Phyllomedusa* for *Hyla bicolor* Daudin, 1803 (= *Rana bicolor* Boddaert, 1772).

ETYMOLOGY: The generic name is derived from the Greek *phyll*, meaning leaf, and the Greek *Medousa* (Latin *Medusa*), apparently in reference to coelenterate medusae. The name alludes to the gelatinous egg-masses deposited on leaves of trees.

DEFINITION: Frogs of the genus *Phyllo-*

medusa are small to large species and generally have a green dorsum; some change to brown or orange-tan at night. The pupil is vertically elliptical and the iris varies from uniformly silvery white to orange-bronze with black reticulations. The palpebral membrane is not reticulated. The fingers and toes have rudimentary webbing or lack webs entirely; the terminal discs are small. The first toe is shorter than, equal to, or longer than the second toe; in those species having a long first toe, it is opposable to the others. The skin on the dorsum is smooth or rugose with or without osteoderms. Parotoid glands are absent in some species, but in most they are distinct and elevated. There is no integumentary-cranial co-ossification. The vocal sac is single, median, and subgular, or absent. The tongue is lanceolate and free posteriorly. Breeding males have brown horny nuptial excrescences on the thumbs. The skull is moderate to deep; the depth is more than 38 per cent of the length (figs. 42 and 43). The parietal plane is barely inclined anteroventrally. The skull is characterized by a frontoparietal fontanelle (narrow and elongate in some species and large and ovoid in others) and moderately developed squamosals with long posterior arms and short anterior arms that extend no more than one-third of the distance to the maxillaries. The quadratojugs are moderately robust or slender; in some small species they are not in bony contact with the maxillaries. The alary processes on the premaxillaries are well developed and extend dorsally or slightly posterodorsally. The maxillary bears a deep pars facialis, which in some species (small species are the exception) extends dorsally at the level of the palatine and connects with the short maxillary process of the nasal (fig. 42). The nasals are large, usually narrowly separated medially, and narrowly separated from, or in bony contact with the sphenethmoid. The canthal ridge is approximately parallel to the maxillary. The maxillary process of the nasal does not extend to the main axis of the maxillary, but is separated from the maxillary (fig. 43) or connects with the posterior process of the pars facialis. The sphenethmoid is well ossified. The dentigerous processes of the pre-momers are reduced or short and situated at a

slight angle or perpendicular to the midline. The pterygoids are robust and lack a bony connection with the prootics. The otic region is relatively small to moderate in size. Teeth

are present on the premaxillaries and maxillaries and lacking on the palatines and parasphenoid in all species, whereas prevomerine teeth are present in some species and absent in others. The teeth are spatulate and bifid. The tadpoles have a ventral spiracle that is sinistral to the midline. Most of the known tadpoles are pelagic types with anterior mouths, deep fins, and slender caudal musculature. Some, such as those of *P. cochranæ* live in streams and show modifications for the stream environment. The mating call in those species having a voice is a single or double, relatively short, poorly modulated note. The haploid number of chromosomes is 13 (known only in *P. lemur* and *venusta*).

COMPOSITION OF THE GENUS: Thirty-one species are currently recognized in the genus; one of these, *P. burmeisteri*, contains two subspecies. Several species groups are recognizable in the genus; generic names have been proposed for some of these groups (see following section on Discussion). Most of the species inhabit South America; only two species, *P. lemur* and *venusta*, occur in Central America. Of these, 196 preserved frogs, seven skeletons, and two lots of tadpoles have been examined.

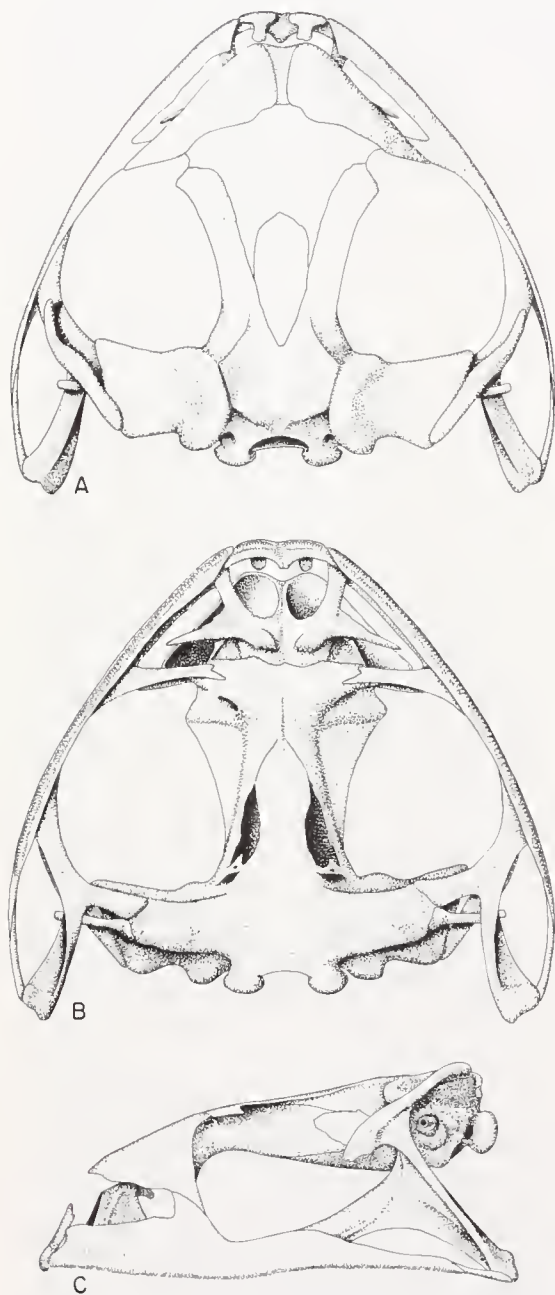


FIG. 42. Dorsal (A), ventral (B), and lateral (C), views of the skull of *Phyllomedusa venusta*, K.U. No. 96514. $\times 2.5$.

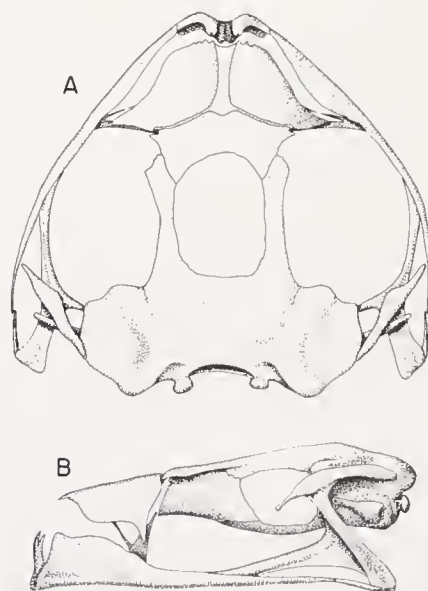


FIG. 43. Dorsal (A), and lateral (B), views of the skull of *Phyllomedusa lemur*, K.U. No. 68629. $\times 5$.

ANALYSIS OF CHARACTERS: The two Middle American species of *Phyllomedusa* are representatives of two widely divergent species groups within the genus. Osteologically, *P. lemur* differs from *venusta* by having relatively less cranial ossification. Any meaningful analysis of characters must include the many South American species; such an account is beyond the scope of the present work.

DISTRIBUTION: The combined geographic ranges of the species of *Phyllomedusa* include the forested lowlands and moderate elevations on South America east of the Andes from the Caribbean (including Trinidad) to northern Argentina; in Central America the genus occurs in Costa Rica and Panamá.

DISCUSSION: Included in the genus *Phyllomedusa* are several large species, such as *bicolor*, *blombergi*, *edentula*, *orcesi*, and *venusta*; these species seem to form a natural group. Probably certain other species, such as *burmeisteri*, *trinitatus*, and *vallanti*, belong with the preceding group. All of these species fit into a pattern of progressive specialization of the hands and feet for grasping.

Several small species (*ayeaye*, *centralis*, *cochranae*, *guttata*, *hypochondrialis*, and *rohdei*) have highly developed grasping feet. These species form a second, apparently natural, group within the genus. Lutz (1966) resurrected *Pithecopus* Cope, 1866, for this group, but she also included such diverse species as *tomopterna*, *trinitatus*, and *vallanti* in *Pithecopus*, thereby making the genus an unnatural and undefinable assemblage of species (see Duellman, 1968b).

Funkhouser (1962) noted that three small, relatively unspecialized species [*lemur*, *loris* (= *buckleyi*), and *medinae*] seem to form a natural group that is distinct from other groups within the genus *Phyllomedusa*.

Perhaps some, or all, of these species groups should be accorded generic status. However, an accurate assessment of variation and relationships must await the accumulation of much more data on most of the South American species, some of which are known only from the types.

The two Central American species obviously are post-Pliocene immigrants from South America. Furthermore, the two species are members of diverse species groups, which

must have differentiated in South America prior to invading Central America.

Phyllomedusa lemur Boulenger

Phyllomedusa lemur Boulenger, 1882a, p. 425 [holotype, B.M.N.H. No. 1947.2.22.37 from "Costa Rica"; Higgins collector]. Taylor, 1952c, p. 809. Funkhouser, 1957, p. 31. Duellman, 1968b, p. 6.

Agalychnis lemur: Cope, 1887, p. 15 [transfer of *Phyllomedusa lemur* Boulenger, 1882a, to *Agalychnis* Cope, 1865a]. Günther, 1901 (1885-1902), p. 291.

DIAGNOSIS: This small phyllomedusine frog can be distinguished from other Middle American members of the subfamily by lacking vomerine teeth, paratoid glands, and webbing on the hands and feet and by having the first toe shorter than, and not opposable to, the second. By day *lemur* is pale green; at night it is orange-tan or brown. *Agalychnis saltator* undergoes the same change in coloration. The latter can be readily distinguished from *lemur* by the presence of webbing and vomerine teeth and by having a red, instead of silvery white, iris. The only other Middle American phyllomedusine lacking webs is *venusta*, which is much larger and has the first toe longer than, and opposable to, the second and paratoid glands forming an elevated dorsolateral ridge. The diurnal coloration of *lemur* is much like that of *Hyla uranochroa*, a species having a horizontal pupil, red iris, and webbing.

DESCRIPTION: This is a small species of *Phyllomedusa*; males attain a maximum snout-vent length of 40.8 mm., and females reach 50.6 mm. In a series of 20 males from Tapantí, Cartago Province, Costa Rica, the snout-vent length is 30.1 to 34.7 (mean, 32.5) mm. The ratio of the tibia length to snout-vent length is 0.483 to 0.550 (mean, 0.513); the ratio of the foot length to snout-vent length is 0.320 to 0.357 (mean, 0.330); the ratio of head width to snout-vent length is 0.294 to 0.349 (mean, 0.315); and the ratio of the diameter of the tympanum to that of the eye is 0.351 to 0.511 (mean, 0.416). Two females from the same locality have snout-vent lengths of 39.5 and 41.6 mm. They do not differ significantly from the males in proportions, except that the ratio of the diameter of the tympanum to that of the eye is somewhat larger, 0.465 and 0.487. Specimens from

TABLE 13

Comparison of Size and Certain Proportions, with Means in Parentheses,
of Four Samples of *Phyllomedusa lemur*.

Locality	Sex	N	Snout-vent Length	Tibia Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
Costa Rica: Tapantí	♂	20	30.1-34.7 (32.5)	0.483-0.550 (0.513)	0.294-0.349 (0.315)	0.351-0.511 (0.416)
Panamá: Río Changena	♂	7	30.7-37.5 (35.1)	0.524-0.575 (0.550)	0.317-0.349 (0.332)	0.372-0.444 (0.393)
	♀	5	43.6-46.8 (44.7)	0.512-0.561 (0.539)	0.312-0.338 (0.328)	0.412-0.531 (0.463)
Panamá: Cerro La Campana	♂	2	38.1-40.8 (39.5)	0.538-0.556 (0.547)	0.318-0.326 (0.322)	0.386-0.419 (0.402)
Panamá: Cerro Malí	♀	1	50.6	0.530	0.310	0.577

the eastern part of the range (central and eastern Panamá) are noticeably larger than those from the western part of the range in Costa Rica and western Panamá. Furthermore, in the eastern part of the range the tibia is relatively longer, and the head is relatively wider than in Costa Rican specimens (table 13).

The head is as broad as the body; the top of the head is barely convex. The eyes are large and prominent. In dorsal and lateral profiles, the snout is truncate. The snout is moderately long; the nostrils are not protuberant and are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is flat, and the lips are not flared. A moderately heavy dermal fold extends posteriorly from the posterior edge of the eye, above the tympanum, and curves downward to a point above the insertion of the arm. The fold covers the upper part of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately long; the upper arm is slender and the forearm is robust. The fingers are relatively short and robust and bear large discs; the diameter of the disc on the third finger is slightly larger than that of the tympanum. The subarticular tubercles are large and round; none is bifid. The supernumerary tubercles are small, low, and indistinct; they are present only proximally. The prepollex is moderately enlarged and in

breeding males bears only a horny nuptial excrescence. A rudimentary web is present between the second and third fingers and in some specimens, between the third and fourth fingers (fig. 44A). The legs are short and slender; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the anterior corner of the eye. A tubercle is present on the heel; a distinct tarsal fold is absent, although a weak fold is present distally in some specimens. No distinct metatarsal tubercle is present. The toes are long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are large and round. Supernumerary tubercles are small, indistinct, and arranged in a single row on the proximal segments of each digit. A thin dermal fold is present along the outer edge of the fifth toe. A rudimentary web is present between the toes (fig. 44B).

The anal opening is directed posteroventrally at the midlevel of the thighs. A short anal sheath is present, and the area below the anus bears several large tubercles. The skin on the belly is faintly granular; elsewhere the skin is smooth. The tongue is lanceolate, moderately notched behind, and free posteriorly for about half of its length. The choanae are longitudinally elliptical. Denticulous processes of the prevomers and prevomerine teeth are absent. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and barely distensible.

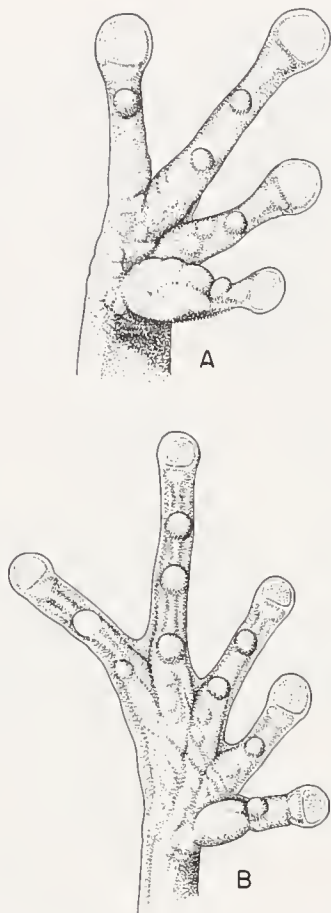


FIG. 44. Hand (A) and foot (B) of *Phyllomedusa lemur*, K.U. No. 63979. $\times 5$.

The general coloration of *Phyllomedusa lemur* by day is pale green (pl. 43, fig. 5). The dorsal surfaces of the body, forearm, fourth finger, thighs, shanks, tarsi, and fourth and fifth toes are pale green. The rest of the hind limbs and the dorsal surfaces of the first three toes are deep orange-yellow. The dorsal surfaces of the upper arms are dark yellow. The flanks are yellow, and the ventral surfaces of the arms, hands, and feet are pale

pinkish cream. The belly is creamy white, and the chin, upper and lower lips, outer edge of tarsi, and outer edge of forearm, are white. At night, the dorsum varies from reddish brown to lavender brown; the thighs and arms are deep yellow, and the venter is white. In some specimens pale green flecks are present on the dorsum (pl. 43, fig. 2). The iris is silvery bronze with a black periphery.

In preservative the dorsum varies from lavender to bluish gray with or without small dark lavender-brown spots. The hidden surfaces of the limbs and the ventral surfaces are creamy white.

TADPOLES: A tadpole in developmental stage 31 has a body length of 16.5 mm. and a total length of 44.0 mm. The body is slightly wider than deep. It is deepest and widest at about two-thirds of the length of the body. The nostrils are dorsolateral about three-fourths of the length of the body. The nostrils are dorsolateral about three-fourths of the distance from the eyes to the tip of the snout and are directed anteriorly. The eyes are dorsolateral and directed laterally. The spiracle is ventral and sinistral to the midline; the spiracular opening is directed posteriorly at a point about midlength of the body. The mouth is anteroventral and directed anteriorly. The cloacal tube is short and dextral to the caudal fins. The caudal musculature is slender and distally tapered nearly to reach the tip of the fin. At midlength of the tail the dorsal, ventral fin, and caudal musculature are of equal depth. The dorsal fin is deepest at about two-thirds of the length of the tail and extends on to the body. The ventral fin is of uniform depth on the anterior half of the tail. Distally the tail curves dorsally, and both fins narrow to a distal point (fig. 45).

In preservative the top of the head is brown; the sides and venter are purplish gray, and the caudal musculature is cream, all with

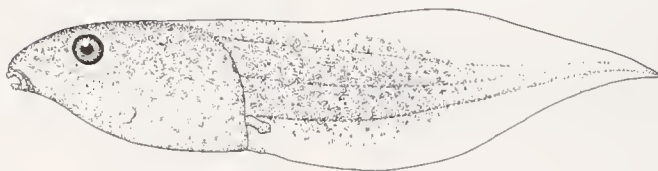


FIG. 45. Tadpole of *Phyllomedusa lemur*, U.S.C. No. 290. $\times 2$.

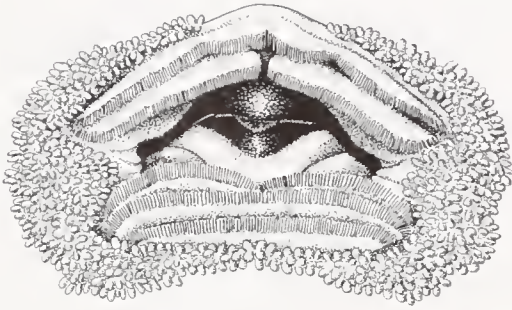


FIG. 46. Mouth of tadpole of *Phyllomedusa lemur*, U.S.C. No. 290. $\times 15$.

brown flecks and reticulations. The caudal fin is transparent with minute brown flecks.

The mouth has a shallow lateral fold. The median part of the upper lip is bare. Otherwise, the mouth is bordered by two or three rows of small labial papillae; numerous papillae are closely packed in the lateral fold. The upper beak is moderately deep and forms a broad arch. The lower beak is not so robust; both beaks are finely serrate. There are two upper and three lower rows of teeth. The two upper rows are of equal length and extend laterally to the papillae. The second row is narrowly interrupted medially. The three lower rows are continuous; the first and second rows are nearly as long as the upper rows, whereas the third row is slightly shorter (fig. 46).

MATING CALL: The call of *Phyllomedusa lemur* consists of a short "tlack." The note is repeated at intervals of eight to 40 seconds. Each note has a duration of 0.20 to 0.29 (mean, 0.25) of a second. The pulse rate is 97 to 118 (mean, 108) pulses per second. The fundamental frequency varies from 108 to 120 (mean, 114) cycles per second, and the dominant frequency varies from 2272 to 2520 (mean, 2396) cycles per second (pl. 35, fig. 2).

NATURAL HISTORY: *Phyllomedusa lemur* inhabits humid lower montane forests having an equable amount of rainfall throughout the year. Consequently, the frogs are active most of the year. Despite their prolonged period of activity, breeding seems to be concentrated in the months of April through July. Males call from the branches of bushes and low trees above shallow ponds.

REMARKS: One specimen is known from eastern Panamá (U.S.N.M. No. 151079 from Cerro Malí, Darién Province). This specimen is much larger than any other known individual of *P. lemur*. This specimen seems to represent a continuation of the west-east cline for an increase in size. Funkhouser (1962, p. 588) named *Phyllomedusa medinae* from Rancho Grande, Estado Aragua, Venezuela. She diagnosed the new species as being much like *P. lemur* and *loris*; *medinae* is about the same size as the large individual of *lemur* from Cerro Malí; the holotype of *medinae*, an adult male, has a snout-vent length of 40 mm. whereas a female (S.U. No. 20379) has a snout-vent length of 49 mm., only slightly smaller than the snout-vent length of 50.6 mm. of the specimen from Cerro Malí. The dorsal coloration of *Phyllomedusa medinae* includes white spots and dark flecks. Dark flecks are present in *P. lemur*, but white spots are absent. Possibly additional material from eastern Panamá and northern Colombia will show that *lemur* and *medinae* are conspecific.

ETYMOLOGY: The specific name *lemur* is Latin and refers to the walking gait of this frog, which is not unlike that of the small monkey-like mammals, the lemurs.

DISTRIBUTION: *Phyllomedusa lemur* occurs in forested regions at elevations of 650 to 1600 meters on the Atlantic slopes of the highlands in Costa Rica and western Panamá; this species also occurs on the Pacific slopes on Cerro La Campana and Cerro Malí in Panamá (fig. 47).

See Appendix 1 for the locality records of the 200 specimens examined.

Phyllomedusa venusta Duellman and Trueb

Phyllomedusa venusta Duellman and Trueb, 1967, p. 128 [holotype, K.U. No. 96150 from approximately 1 kilometer west-southwest of the junction of the Río Mono and the Río Tuira, Darién Province, Panamá, elevation 130 meters; Charles W. Myers collector]. Duellman, 1968b, p. 6.

DIAGNOSIS: This large species belongs in that group of *Phyllomedusa* having the first toe longer than the second, possessing vomerine teeth and large parotoid glands, and lacking webbing on the hands and feet. *Phyllomedusa venusta* is distinguished from other members of the group by having the following combination of characters: skin of dorsum

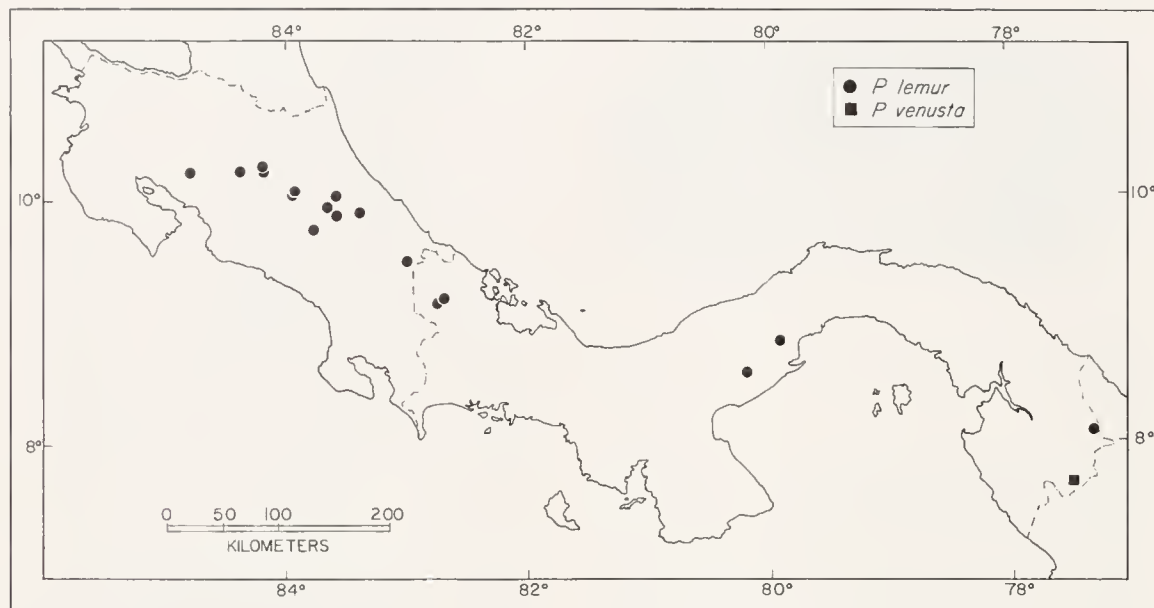


FIG. 47. Distribution of Middle American species of *Phyllomedusa*.

pustulate, parotoid glands forming an angular ridge anteriorly and extending posteriorly nearly to the groin, chin and chest dark brown with white median spot, ventral and posterior surfaces of thighs brown with a white spot ventrolateral to the anus, and belly orange. *Phyllomedusa venusta* differs from the other Central American species, *lemur*, by having well-developed parotoid glands, the first toe longer than, and opposable to, the second, and in size. *Phyllomedusa lemur* is a small species lacking parotoid glands and having the first toe shorter than, and not opposable to the second.

DESCRIPTION: Males of this large species attain a maximum snout-vent length of 86.3 mm.; the only known female has a snout-vent length of 97.7 mm. Three adult males from eastern Darién Province, Panamá, have snout-vent lengths of 74.6 to 86.3 (mean, 82.0) mm.; the ratio of tibia length to snout-vent length is 0.450 to 0.479 (mean, 0.465); the ratio of foot length to snout-vent length is 0.330 to 0.369 (mean, 0.349); the ratio of head length to snout-vent length is 0.327 to 0.346 (mean, 0.333); the ratio of head width to snout-vent length is 0.334 to 0.353 (mean, 0.341), and the ratio of the diameter of the tympanum to

that of the eye is 0.577 to 0.607 (mean, 0.591). The female differs by having a larger tympanum; the tympanum/eye ratio is 0.633.

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is acuminate. In lateral profile, in males, the snout gradually slopes from the eyes to the nostrils and then curves in a sharp incline to the tip of the snout, whereas in females it is truncate. The canthus is elevated and rounded. The nostrils are barely protuberant and are situated slightly closer to the tip of the snout than to the eyes. The loreal region is concave, and the lips are moderately heavy and not flared. There is no dermal fold behind the eye. The tympanum is distinct, although the dorsal and posterior edges are covered by skin. The tympanum is posterior to the eye and separated from it by a distance equal to the diameter of the tympanum.

The upper arm is slender, and the forearm is moderately robust. A row of tubercles is present on the ventrolateral edge of the forearm. The fingers are long and lack webbing (fig. 48A). The fourth finger is barely shorter than the third. The discs are small; none is as large as the tympanum. The subarticular tubercles are large and conical. Two flat,

round, palmar tubercles are present, and one large elliptical tubercle is present on the base of the pollex. The pollex is slightly larger in males and bears a smooth, horny nuptial excrescence. The hind limbs are relatively short and moderately slender. The heels of the adpressed limbs barely overlap; the tibiotarsal articulation extends to the posterior corner of the eye. Dermal flaps or tubercles on the heel are lacking, and the tarsal fold is absent. The inner metatarsal tubercle is flat, ovoid, and not visible from above. The toes are moderately long, slender, and unwebbed (fig. 48B). The discs are slightly smaller than those on the fingers. The subarticular tubercles are large and conical.



FIG. 48. Hand (A) and foot (B) of *Phyllomedusa venusta*, K.U. No. 96150. $\times 3$.

No distinct anal flap is present; the anal opening is directed posteroventrally at the level of the middle of the thighs. The skin on the dorsum and flanks is pustulate. The pustules are raised but flat, not conical. The dorsal surfaces of the forearms and dorsal and ventral surfaces of the hind limbs are tuberculate; tubercles are arranged in rows on the edges of the shanks and tarsi. The skin on the throat, chest, belly, and underside of the forelimbs is granular. A large parotoid gland extends from the eye nearly to the groin. The gland forms an angular, longitudinal ridge on the anterior half of the body and a rounded ridge posteriorly. A large glandular area is present on the side of the neck above the insertion of the arm. The tongue is lanceolate and twice as long as wide; it is shallowly notched posteriorly and free behind for about one-third of its length. The dentigerous processes of the prevomers are small and postero-medially inclined between the small, ovoid, choanae. The males have five teeth on each prevomerine process; the female has three and four teeth on each prevomerine process. Vocal slits and a vocal sac are absent.

The general coloration is green above and brown on the throat and chest and orange on the belly (pl. 41, fig. 2). The dorsum is uniform green, darkest on the dorsal part of the body and somewhat paler on the shanks, tarsi, forearms, and sides of the head. The flanks are green with minute pale blue flecks, especially in the groin. The chin, chest, anterior part of the belly, and the ventral surfaces of the thighs are dark grayish brown with white spots. One large spot is present on the proximal ventral surface of the thighs in all specimens. In one individual, a series of smaller spots is present more distally on the thigh. All specimens have a white spot anteromedially on the chest; one individual has several smaller spots on the throat and chest, and another has two small spots on the throat (fig. 49). The posterior part of the body is pale, dull orange; some orange flecks are present on the posterior surfaces of the thighs. The anterior surfaces of the thighs and tarsi, ventral surfaces of shanks, and distal phalanges of the first and second fingers and first, second, and third toes are pale pinkish orange with dull greenish brown markings.

The ventral surfaces of the hands and feet are white. A white stripe extends along the edge of the lower lip and continues around the base of the arm to a point about mid-length of the shank. A narrow, creamy white or pale yellow stripe is present on the outer edge of the forearm and fourth finger, and a creamy white line is present above the anus. The iris is golden orange with black reticulations. The palpebrum is clear, and the nuptial excrescences are dull grayish brown.

In preservative the dorsum is dark blue and the parotoid glandular areas are slightly darker blue. The flanks are blue with black-bordered white spots. The edge of the lower lip, the stripe on the anterior part of the flank, the stripe along the edge of the forearm, the stripe above the anus, the ventral surfaces of the upper arm, and the median ventral surfaces of the forearm are white. The ventral surfaces of the shank, and anterior surfaces of the thighs are creamy white with

vertical purplish blue bars on the latter. The ventral and posterior surfaces of the thighs and ventral surfaces of the tarsi, forearm, hand, and feet are brown. The chin, chest, and anterior part of the belly are dark brown; the rest of the belly is dull creamy tan.

TADPOLES: The tadpoles of this species are unknown.

MATING CALL: Because vocal slits and a vocal sac apparently are absent, it is presumed that this species has no mating call, but a male emitted a short release call when grasped (pl. 37, fig. 3).

NATURAL HISTORY: The five known specimens were found on vegetation in a swamp, where the species probably breeds, although no breeding activity was noted.

REMARKS: *Phyllomedusa venusta* is the only Central American representative of that group of large *Phyllomedusa* having the first toe longer than the second. The other species are found in South America east of the Andes. The absence of information on the colors in life and on the tadpoles in the majority of these species precludes any meaningful interpretation of interspecific relationships at this time.

ETYMOLOGY: The specific name is derived from the Latin *venustus*, meaning like Venus, beautiful and elegant, and alludes to the coloration of the frog.

DISTRIBUTION: Presently *Phyllomedusa venusta* is known only from eastern Panamá (fig. 47).

See Appendix 1 for the locality records of the five specimens examined.

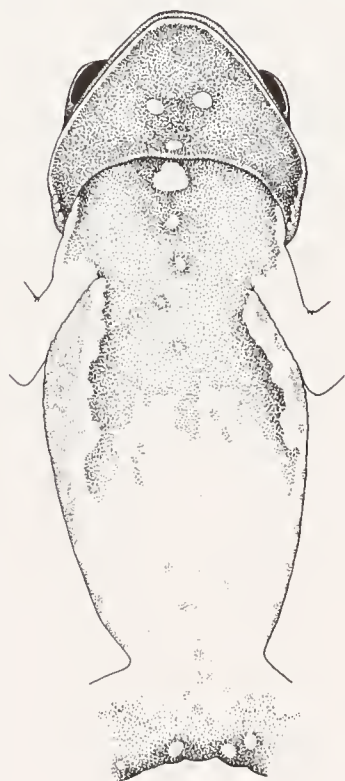


FIG. 49. Ventral coloration in *Phyllomedusa venusta*, K.U. No. 96150. $\times 1$.

Genus *Hemiphractus* Wagler

Hemiphractus Wagler, 1828, column 743 [type species, *Hemiphractus spixii* Wagler, 1830 (= *Rana scutata* Spix, 1824) by subsequent designation (Peters, 1862, p. 146)]. Noble, 1926, p. 19 [synonymy of *Cerathyla* with *Hemiphractus*].

Cerathyla Jiménez de la Espada, 1871, p. 63 [type species *Cerathyla bubalus* Espada, by subsequent designation (Myers and Carvalho, 1945, p. 21)].

GENEROTYPE: *Rana scutata* Spix, 1824, by subsequent designation. Wagler, in 1826 and 1830 used the name *Hemiphractus spixii*, which Peters (1862) showed to be the same as *Rana scutata* Spix, 1824. Thus, the species now known as *Hemiphractus scutatus* (Spix) is the generotype.

ETYMOLOGY: The generic name is derived from the Greek prefix *hemi*, meaning half, and the Greek *phraktos*, meaning protected, and refers to the helmet covering what seems to be about the anterior half of the animal.

DEFINITION: Frogs of the genus *Hemiphractus* are of medium size and have a large triangular head modified into a bony helmet. Dermal appendages are present on the eyelids and tip of the snout in some species. The skin is partially adherent to the neural spines, which are conspicuous dorsally. Webbing is lacking on the hands and feet. The dorsum is variously mottled tan, brown, or olive. The pupil is horizontal, and the palpebral membrane is clear. The vocal sac is single, median, and subgular. Breeding males apparently lack horny nuptial excrescences. The skin on the dorsum is smooth and not co-ossified on the head.

The skull is highly modified, nearly twice as wide as long, triangular in dorsal view, and nearly completely roofed by moderately rugose bones, which are marked by small, circular pits (fig. 50). The dorsal roofing bones are expanded so as to roof the skull; the nasals and frontoparietals have a common point of suture. Likewise, the premaxillaries, maxillaries, and quadratojugals have broad, thin, dorsal flanges broadly sutured to the dermal roofing bones. Consequently, the orbit is completely bordered by bone. A small fossa is present at the point of junction of the maxillary, quadratojugal, and squamosal. The posterior arm of the squamosal is greatly expanded into a posterolateral process or "horn." The prevomer is a slender arcuate bone bearing odontoids but lacking teeth. The robust, transverse palatines bear odontoids and nearly meet medially. The pterygoid is exceptionally robust and fully articulated to the maxillary, squamosal, and prootic. The parasphenoid has long alary processes and lacks odontoids. The mandible is strong, and the dentary bears odontoids, the anterior one of which is greatly enlarged. Teeth are present on the maxillaries and premaxillaries.

The known life histories indicate that the young develop directly from eggs carried on the back of the female. The mating calls and number of chromosomes are unknown.

COMPOSITION OF GENUS: Probably five species are recognizable in the genus; all are considered to be monotypic. Only one species occurs in Central America; of it, 33 preserved frogs and two skeletons have been examined.

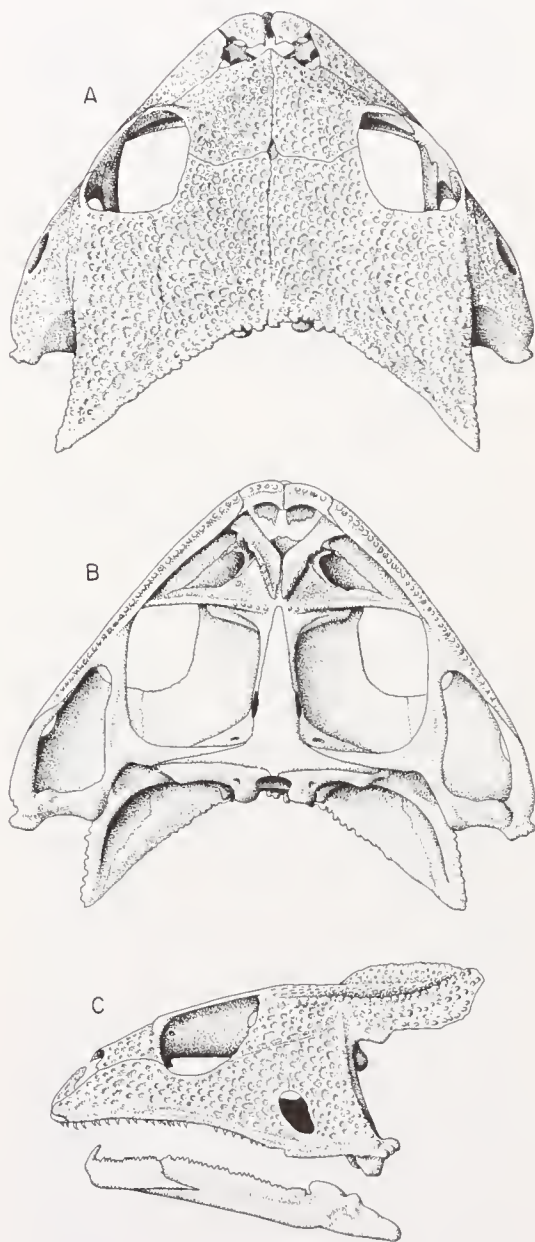


FIG. 50. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Hemiphractus panamensis*, K.U. No. 93509. $\times 2$.

DISTRIBUTION: Upper Amazon Basin from Peru northward, Pacific slopes of Colombia and northwestern Ecuador, Pacific and Caribbean slopes in eastern Panamá, and Caribbean slopes in western Panamá and probably adjacent Costa Rica.

DISCUSSION: Although Noble (1926, p. 19) considered *Cerathyla* to be a synonym of *Hemiphractus*, most subsequent workers have recognized two genera. The latter genus lacks expanded digital pads and has the eyes somewhat closer to the snout than in *Cerathyla*, which has expanded digital pads. Dr. Alan E. Leviton has been studying these frogs for a number of years and has strongly advised that *Ceratothyla* should not be recognized. cursory examination of some of the species and selected skeletal material, including *Hemiphractus scutatus*, indicates that Leviton's suggestion is reasonable.

Hemiphractus panamensis (Stejneger)

Cerathyla panamensis Stejneger, 1917, p. 31 [holotype, U.S.N.M. No. 55320 from Signal Loma, 5 kilometers south of Santa Isabel, Colón Province, Panamá; Charles G. Holland collector].

DIAGNOSIS: This moderate-sized species differs from all other members of the genus by the following combination of characters: helmet rugose, posterior border of helmet deeply indented, dermal flaps present on upper eyelid, moderately long dermal proboscis triangular in section, and calcars present. *Hemiphractus panamensis* is immediately distinguishable from other Middle American hylids by having a large triangular helmet lacking co-ossification and by having the skin partially adherent to the neural spines of the vertebrae.

DESCRIPTION: Males of this medium-sized species attain a maximum snout-vent length of 56.3 mm.; and females reach 58.7 mm. In a series of 11 males from the Serranía de Pirre, Darién Province, Panamá, the snout-vent length is 48.5 to 56.3 (mean, 52.8) mm.; the ratio of tibia length to snout-vent length is 0.473 to 0.530 (mean, 0.506); the ratio of foot length to snout-vent length is 0.428 to 0.479 (mean, 0.455); the ratio of head length to snout-vent length is 0.422 to 0.458 (mean, 0.442); the ratio of head width to snout-vent length is 0.451 to 0.511 (mean, 0.489), and

the ratio of the length of the tympanum to that of the eye is 0.740 to 0.980 (mean, 0.874). Five females from the same locality have snout-vent lengths of 63.0 to 68.7 (mean, 66.0) mm. and much smaller tympani; the ratio of the length of the tympanum to the diameter of the eye is 0.523 to 0.667 (mean, 0.580).

The head is as wide as, or slightly wider than, the body. The top of the head is smooth; the temporal region is greatly expanded posterolaterally to form a point. The width of the head between the points is less than the width at the angles of the jaws; the ratio of the two measurements varies from 0.740 to 0.932 (mean, 0.874). In dorsal profile the snout is acuminate; in lateral profile, the snout slopes from the interorbital region to the margin of the lips. The canthus is barely evident and rounded; the loreal region is slightly concave and inclined laterally to the margins of the lips. A bony ridge extends from the posterior corner of the eye to the tip of the posterolateral point of the skull. The tympanum is entirely distinct and much higher than long. The tympanum is directed posterolaterally and is separated from the eye by a distance equal to twice the length of the tympanum. A large, triangular, dermal flap is present below the tympanum at the angles of the jaws. A large, fleshy, tubercle is present on the edge of each upper eyelid, and a pointed, fleshy, triangular (in transverse sections) proboscis is present. The eyes are relatively small and widely separated, and the nostrils are directed anterodorsally at a point about midway between the eyes and the tip of the snout.

The arms are moderately long and robust; an axillary membrane is absent. A small tubercle is present on the ventral surface of the elbow, and a low, fleshy fold extends along the ventrolateral edge of the forearm. There is no transverse dermal fold on the wrist. The fingers are long and moderately slender and bear small discs; the width of the disc on the third finger is slightly less than the length of the tympanum. The thumb is longer than the second finger. The subarticular tubercles are moderately large and conical; in some individuals, the distal tubercle on the third and fourth fingers are distinctly bifid. The super-

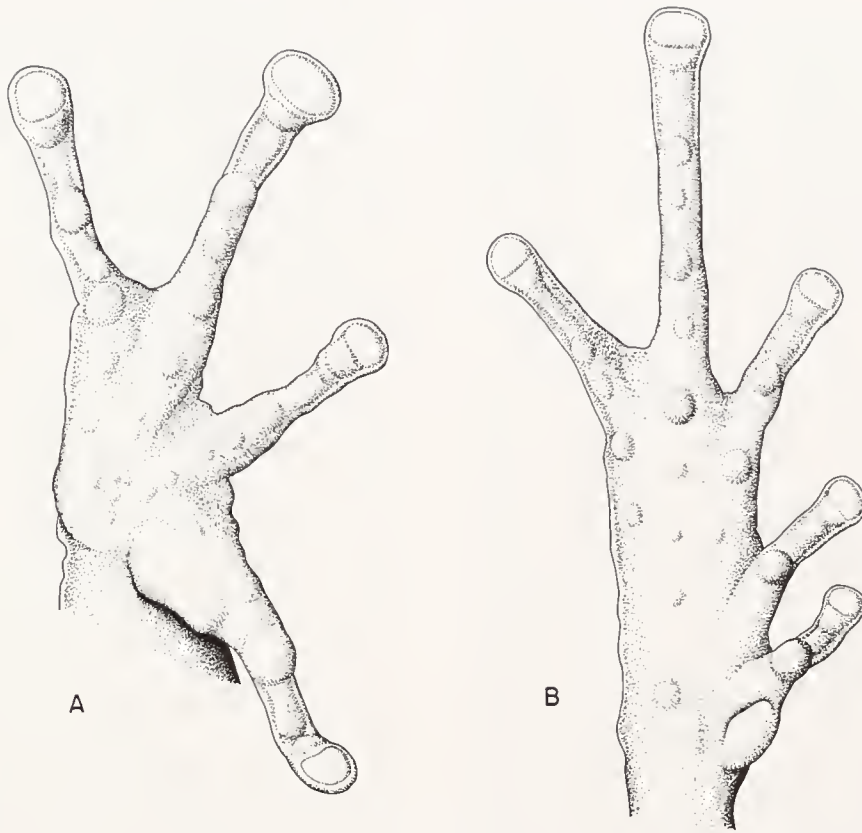


FIG. 51. Hand (A) and foot (B) of *Hemiphractus panamensis*, K.U. No. 107417. $\times 3$.

numerary tubercles are conical; they are distinct in some specimens and barely evident in others. A low, indistinct, palmar tubercle is present. The prepollex is moderately enlarged and in breeding males does not bear a horny nuptial excrescence. A vestige of a web is present between the second and third and between the third and fourth fingers (fig. 51A). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A fleshy calcar is present on the heel, but a tarsal fold is lacking. The inner metatarsal tubercle is elongately ovoid and elevated; a small subconical outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are large and conical; and the super-

numerary tubercles are high and conical. The toes are webbed basally (fig. 51B).

The anal opening is directed posteriorly near the upper level of the thighs; the opening is covered by a broad, fleshy sheath. The skin on the belly is granular; that on the dorsum of the body and shanks and on the ventral surfaces of the limbs is smooth. The skin on the dorsal surfaces of the forearms, thighs, and flanks is tubercular. The skin on the head is not co-ossified with the underlying bones. The skin is partially adherent to the neural processes of the vertebrae, which are prominent dorsally. The tongue is broadly cordiform, shallowly notched behind, and barely free posteriorly. The palatines form a transverse ridge across the roof of the mouth. The prevomers form a pair of posteromedially inclined processes between the small, ovoid choanae. Odontoids are present on palatines and prevomers; likewise, small serrations are

present on the dentary and a pair of large odontoids are present at the symphysis of the lower jaws. The vocal slits are small and nearly transverse near the angles of the jaws. The vocal sac is single, median, subgular.

The general coloration of *Hemiphractus panamensis* usually consists of a pale brown dorsum with darker brown markings (pl. 44, fig. 2). The dorsum varies from pale yellowish tan to grayish brown or olive-gray. Dorsal markings vary from just a few small dark flecks to one or two chevron-shaped marks and/or a dark brown dorsolateral stripe. In most individuals dark transverse bands are evident on the dorsal surfaces of the limbs. The posterior surfaces of the thighs are dark brown with a diffuse creamy yellow stripe separating the dark color on the posterior surfaces of the thighs from the coloration on the dorsal surfaces. The throat and chest are dark brown or black. A white spot is present medially on the chest; in many individuals this is extended anteriorly to form a median stripe or series of dashes on the throat. There are some small white spots on the lower lip and a few white tubercles on the chest. The rest of the venter is brown with an orange tint. The tongue and the lower inside edge of the lip is yellowish orange. The iris is gray with a yellowish cast above and a pale red dish brown suffusion below and a narrow horizontal brown stripe through the pupil. The palpebral membrane is clear.

Small individuals tend to have paler and more contrasting patterns than do large adults. Some large females are nearly uniform dark grayish brown above. The coloration of the upper part of the iris varies from yellow to pale green.

In preservative the dorsum is tan to dark brown with darker brown markings evident or not. The venter is brown with white flecks and spots, and the posterior surfaces of the thighs are dull brown.

TADPOLES: *Hemiphractus panamensis* has direct development of the young, which are discussed in a following section on natural history.

MATING CALL: No recordings of the call of this species are available. Myers (1966, p. 71) noted that one individual emitted a loud cat-like squall when handled and that

similar noises were heard from several individuals in a bag.

NATURAL HISTORY: *Hemiphractus panamensis* inhabits humid montane or cloud forests characterized by an abundance of atmospheric moisture throughout the year. The frogs are always found either on the ground or relatively close to the ground. Some individuals have been found in leaf litter on the forest floor by day. Individuals observed at night usually are on sticks, leaves or ferns at a height of less than one meter above the ground. However, one individual was found on a tree trunk about two meters above the ground, and another at a similar height was looking out from the base of a bromeliad on a tree trunk at night. These observations indicate that the frog is nocturnal and that it seeks shelter amidst the leaf litter on the forest floor by day.

One individual having a snout-vent length of 48.5 mm. contained an adult dendrobatid frog (*Colostethus pratti*) and a gastropod having a diameter of 10 mm. Another individual having a snout-vent length of 50.4 mm. contained an adult *Ptychoglossus festae*. Both *Colostethus* and *Ptychoglossus* are principally diurnal; the appearance of these species in the diet of *Hemiphractus* is an apparent contradiction to the nocturnal habits of the species as evidenced by our observations in the field. Both of the prey items inhabit the leaf litter on the forest floor; perhaps, in the early morning hours or at dusk the activity of the animals overlap that of *Hemiphractus*. Furthermore, it is entirely possible that *Hemiphractus* in some cases, is active, perhaps only on the forest floor by day. On the other hand, possibly *Hemiphractus* feeds on such prey when they are sleeping.

Myers (1966, p. 70) described the aggressive behavior in this species: "These frogs made no attempt to escape unless unduly prodded. Rather, when picked up or tapped on the snout, they gaped their mouth and sometimes slightly arched the body by throwing the head up and back. The effect was striking owing to a bright yellow-orange tongue (yellow in one), as well as to the large mouth and wierd head shape. . . . The display is not all bluff, for several readily bit any object placed close to the mouth, and one

even fastened its jaws around the head of a neighboring *Cerathyla* [= *Hemiphractus*]. By offering a finger to the first *Cerathyla* captured, I was made painfully aware of the two sharp odontoids (on front of lower jaw) that proved capable of piercing human flesh; one must wait patiently for the grip to be released, else pry apart the jaws." Additional observations on this species in Panamá substantiate the behavior reported by Myers, who made the point that the bright yellow-orange tongue is an integral part of the mouth-gaping behavior.

In this species, the female carries the eggs on the back in the manner described for *Hemiphractus bubalus* described by Boulenger (1903). The eggs apparently encapsulate on the dorsum and adhere strongly to the skin. The resulting modification of the dermis of the dorsum consists of a series of depressions (pl. 7), which apparently are extremely superficial, because the skin of the back, containing these scars is sloughed off after the young have departed (Stejneger, 1917, p. 33). The number of scars on the back of two females (U.S.N.M. No. 55320 with a snout-vent length of 60.0 mm., and B.Y.U. No. 19142 with a snout-vent length of 61.2 mm.) is 14 and 12, respectively. Another female (K.U. No. 93503 with a snout-vent length of 58.7 mm.) contained twelve large, yolked eggs with an average diameter of about 6 mm.

Noble (1917, p. 808) reported on a histological examination of the gills and their attachment in the specimens reported by Stejneger (1917). Examination of the female collected more recently (B.Y.U. No. 19142) substantiates the data presented by Noble and provides some further information. At the time that I examined this specimen (January 18, 1968), two young were attached to the female and five additional young were contained in the jar with the female. The back of the female is deeply pitted; the gills of each juvenile frog are embedded in these pits; two pairs of white cords extend from the gills to the throat of the froglet (pl. 2). In a froglet having a snout-vent length of 15 mm., the cords are about 7 mm. in length and attached to the disc-like gill that is about 6 mm. in diameter. Superficially, the gills appear to be attached to the frog by two cords, but careful

examination reveals that what appears to be a single cord is actually a pair of closely associated cords. The cord enters the throat on either side of the hyoid and just anterior to the pectoral girdle. The gills are closely adherent to the disc-like base of the depression in the back of the female; the gills seemingly are separated from the skin by a thin gelatinous layer, which Noble (1917, p. 808) stated to be the egg membranes.

Noble showed that the cord contained blood vessels and striated muscle and that the blood vessels anastomosed in the gills. Because gills apparently are separated from any vascular tissue in the female, it is most unlikely that the developing frog derives either nourishment or oxygen from the parent. Instead, the gills apparently serve two functions—to obtain oxygen from the atmosphere, and to provide a firm attachment to the female for purposes of transportation.

The young individuals associated with B.Y.U. No. 19142 seem to be nearly fully developed. In each, the cranium is reasonably well ossified; the neural processes of the vertebrae are evident dorsally, and the triangular fleshy proboscis is evident. The eyes are well developed, but a large amount of yolk remains in the gut.

The gills of *Gastrotheca*, the young of which develop within a dermal pouch, function for oxygen exchange with the tissues of the female. Certainly the behavioral trait of carrying the eggs on the back, as it is exhibited by *Cryptobatrachus* and *Hemiphractus*, is advantageous, because the females can provide some care for the eggs. Such parental care may, in fact, be a necessity. Direct development circumvents the disadvantages of an aquatic larval stage; however, the adult frogs are obliged to provide some method of transportation for the developing froglets until they are capable of surviving alone. The gill-attachment observed in *Hemiphractus* obviously is the key to the success of the transportation of the young. The development and exact function of these so-called "gills," be it attachment, respiration, or both, must await the acquisition of additional females with early-term eggs. It will be most interesting to determine whether or not the cords are homologous with the gills of hylid tadpoles.

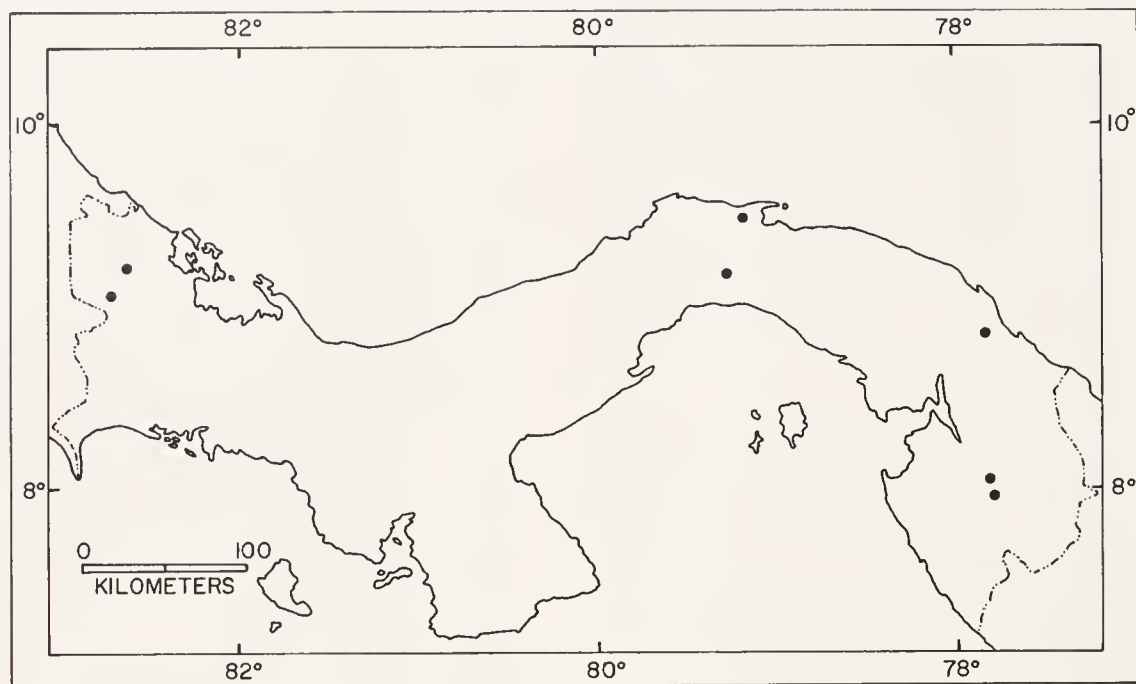


FIG. 52. Distribution of *Hemiphractus panamensis*.

The meager evidence of life history suggests that the breeding season is prolonged in this species. The two females bearing young were collected on May 20 and September 15, whereas the female with large eggs was obtained on December 13.

REMARKS: The taxonomic status of the various named kinds of *Hemiphractus* is open to question; this genus is being studied by Alan E. Leviton, who suggested (*in litt.*) that *Hemiphractus panamensis* probably is most closely related to *fasciatus* on the Pacific slopes of Ecuador; *panamensis* is somewhat intermediate between *prohoscidea* and *fasciatus*.

ETYMOLOGY: The specific name is in reference to Panamá, the country from which the type specimen originated.

DISTRIBUTION: *Hemiphractus panamensis* occurs at elevations between 300 and 1600 meters on the Caribbean slopes of the highlands of Panamá and on the Pacific slopes of the highlands in eastern Panamá (fig. 52). The species is known from the Serranía de Pirre and the Serranía de Darién in eastern Panamá, but it was not found on the Serranía del Sapo.

See Appendix 1 for the locality records of the 35 specimens examined.

Anothea Smith

Anothea Smith, 1939, p. 190 [type species by original designation, *Gastrotheca coronata* Stejneger, 1911 (= *Hyla spinosa* Steindachner, 1864)].

GENEROTYPE: *Hyla spinosa* Steindachner, 1864. Günther (1859) assigned juveniles from México and Costa Rica to *Opisthodelphys ovifera* (Lichtenstein and Weinland, 1854), and Boulenger (1882a) assigned the same specimens to *Nototrema oviferum*. Stejneger (1911) had an adult male bearing the characteristic cranial spines and thus was able to demonstrate that the Middle American species was distinctly different from the South American *Opisthodelphys* (= *Gastrotheca*) *ovifera*; he named the Middle American species *Gastrotheca coronata*. Smith (1939) demonstrated that females of *coronata* lacked the pouch characteristic of *Gastrotheca* and proposed the generic name *Anothea* for *coronata*.

Dr. Charles F. Walker called my attention to Steindachner's (1864) description of *Hyla*

spinosa, and Walker, upon examination of the holotype of *spinosa* in Vienna, concluded that it probably was the same as the frogs assigned to *Anothea coronata*. Through the courtesy of Dr. Josef Eiselt, I borrowed the holotype of *Hyla spinosa* and compared it with the numerous examples of *Anothea coronata*. On the basis of the distinctive coloration, structure of the feet, integumentary-cranial co-ossification, and spines on the squamosal (holotype of *spinosa* is a juvenile having a snout-vent length of 40 mm.), there is no doubt that the holotype of *Hyla spinosa* is the same as the frogs that have been called *Anothea coronata*. Consequently, the generic type of *Anothea* is *Gastrotheca coronata* Stejneger, 1911, which is a junior synonym of *Hyla spinosa* Steindachner, 1864.

The type locality of "Brazil" given by Steindachner probably is in error, because the species is unknown south of central Panamá.

ETYMOLOGY: The generic name is derived from the Greek *an-*, meaning without, and the Greek *theke*, meaning container, in reference to the absence of a brood pouch.

DEFINITION: The frogs in this genus are moderately large and are characterized by integumentary-cranial co-ossification and a casqued head that has spines dorsally and is wider than long (fig. 53). The dorsum is brown and the sides and belly are dark brown or black. The pupil is horizontally elliptical, and the palpebral membrane is clear. The fingers essentially lack webbing, and the toes are about one-half webbed. Breeding males lack horny nuptial excrecences on the thumbs. The skin is co-ossified with the underlying cranial elements on the top of the head, except the sphenethmoid, and in the loreal region, but not on the lips. The maxillaries and premaxillaries are unmodified. The skull is completely roofed. The frontoparietals extend laterally over the otic region. The anterior arm of the squamosal extends to, or nearly to, the maxillary. The quadratojugal articulates with the maxillary. Long, slender, pointed, curved spines are present on the canthal ridge of the nasal, outer edges of the frontoparietals, and on the anterior and posterior arms of the squamosals. A few small spines are present on the maxillary below the orbit. The palatine is slender, and the medial

ramus of the pterygoid is robust and in bony contact with the prootic. Narrowly spatulate, bifid teeth are present on the premaxillaries, maxillaries, and prevomers, and absent on the palatines and parasphenoid. The tadpoles develop in bromeliads or water-filled cavities in trees, have two upper and two lower rows of teeth, and feed on frog eggs. The supposed mating call consists of a long series of like notes. The haploid number of chromosomes is 12.

COMPOSITION OF THE GENUS: The genus is monotypic; 200 preserved specimens, five skeletons, and four lots of tadpoles have been examined.

DISTRIBUTION: *Anothea* occurs on the Atlantic slopes of Vera Cruz and Oaxaca, México, on the Caribbean slopes of Costa Rica and western Panamá, and on the Pacific slopes of central Panamá.

DISCUSSION: *Anothea* apparently is closely related to *Gastrotheca*, from which it differs by lacking a brood pouch in the females. The skulls of casque-headed *Gastrotheca*, such as *G. nicefori*, resemble that of *Anothea*, except that the latter has the long spines, which are absent in *Gastrotheca*.

Anothea probably evolved from an early *Gastrotheca* stock that was isolated in Middle America, whereas the main differentiation of *Gastrotheca* took place in South America.

Anothea spinosa (Stejneger)

Opisthodelphys ovifera (nec *Notodelphys ovifera* Lichtenstein and Weinland, 1854): Günther, 1859, p. 117. Brocchi, 1882, p. 47.

Hyla spinosa Steindachner, 1864, p. 539 [holotype, N.M.W. No. 16101 from "Brazil"; Johann Natterer collector].

Nototrema oviferum (part): Boulenger, 1882a, p. 418. Günther, 1901 (1885-1902), p. 288.

Nototrema marsupiatum (nec *Hyla marsupiata* Duméril and Bibron, 1841): Díaz de León, 1904.

Gastrotheca coronata Stejneger, 1911, p. 287 [holotype, U.S.N.M. No. 48279 from Palomo, Valle de Orosi, Cartago Province, Costa Rica; C. Picado T. collector]. Kellogg, 1932, p. 133.

Anothea coronata: Smith, 1939, p. 190 [proposed genus *Anothea* for *Gastrotheca coronata* Stejneger, 1911]. Smith and Taylor, 1948, p. 70. Taylor, 1952c, p. 797.

Anothea spinosa: Duellman, 1968c, p. 195 [synonymized *Gastrotheca coronata* Stejneger, 1911, with *Hyla spinosa* Steindachner, 1864]

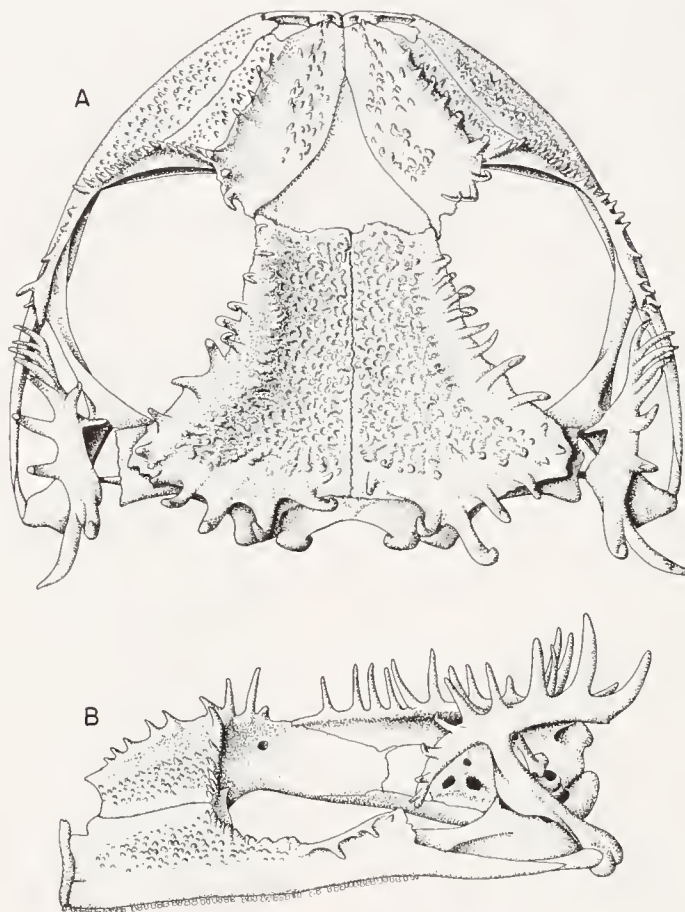


FIG. 53. Dorsal (A) and lateral (B) views of the skull of *Anotheca spinosa*. (K.U. No. 84899). $\times 4$.

DIAGNOSIS: Adults of this species are readily distinguished from all other Middle American hylids by the presence of integumentary-cranial co-ossification in combination with sharp, dorsally pointed, spines on the canthal, supratympanic, and occipital ridges. The diagnostic color pattern of dark brown with black venter and flanks bordered by white is present in small juveniles, which lack the cranial spines.

DESCRIPTION: Males of this species attain a maximum known snout-vent length of 68.5 mm., and females reach 73.0 mm. In a series of 20 males from eastern México, the snout-vent length is 59.8 to 65.1 (mean, 60.7) mm.; the ratio of tibia length to snout-vent length is 0.461 to 0.515 (mean, 0.486); the ratio of foot length to snout-vent length is 0.403 to 0.463

(mean, 0.430); the ratio of head length to snout-vent length is 0.339 to 0.361 (mean, 0.352); the ratio of head width to snout-vent length is 0.339 to 0.373 (mean, 0.357), and the ratio of the diameter of the tympanum to that of the eye is 0.716 to 0.873 (mean, 0.810). Eight females from the same region have snout-vent lengths of 57.7 to 69.6 (mean, 62.2) mm.; in proportions, the females differ from the males only by having slightly larger tympani, 0.714 to 0.938 (mean, 0.833). Few specimens are available from the southern part of the range, where individuals apparently reach a larger size than in the north. The largest specimens of both sexes (male, 68.5 mm. and female, 73.0 mm.) are from Panamá.

The head is about as wide as the body, and the top of the head, between the supra-

orbital ridges, is flat. In dorsal profile, the snout is acutely rounded, and in lateral profile, it is truncate. The skin on the top of the head is co-ossified with the underlying cranial elements, which are modified to form an elevated canthal ridge, a supraorbital ridge, a supratympanic ridge, and a transverse occipital ridge. In large adults dorsally directed spines are present on the supraorbital, supratympanic, and occipital ridges, and in some specimens, low spines are present on the canthal ridges. In some specimens, some or all of the spines are covered by skin, but in some individuals sharp-tipped bony spines protrude through the skin. In juveniles, having snout-vent lengths of less than 25 mm., there is no evidence of bony ridges or of spines. In specimens having snout-vent lengths of 40 to 50 mm., ridges and spines are beginning to develop. For example, one individual having a snout-vent length of 45 mm. has the skin on the top of the head co-ossified with the underlying cranial elements. The canthal ridges and supratympanic ridges are present, and blunt, skin-covered spines are present on the supratympanic ridge. Another individual having a snout-vent length of 47 mm. also has a few small spines in the area of the supraorbital ridges and has a pair of spines on the occiput, but definitive supraorbital and occipital ridges are absent. In large adults having a maximum development of spines a short, spiny postorbital ridge is present. In these specimens, the spines are closely placed and continuous from the nostrils along the canthal, supraorbital, and supratympanic ridges to the transverse occipital ridge (fig. 54). In some specimens, minute spines are present medial to the primary row of spines. The snout is moderately long, and the nostrils are barely protuberant and situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The internarial region is slightly depressed. The loreal region is concave, and the lips are moderately thick and slightly flared. In large adults the skin is co-ossified in the loreal region but not on the lips. The upper part of the tympanum is concealed by the supratympanic ridge; otherwise, the tympanum is distinct and elevated; it is separated from the eye by a distance equal to

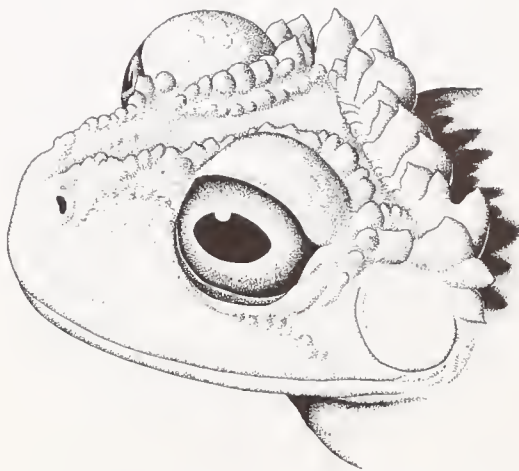


FIG. 54. Head of *Anotheca spinosa* (K.U. No. 58076) showing extreme condition of cranial spines. $\times 3$.

about three-fourths of the diameter of the tympanum.

The arms are long and slender; there is no row of tubercles along the outer edge of the forearm, but a weak transverse dermal fold is present on the wrist. The fingers are long and slender and bear moderately large discs; the width of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The subarticular tubercles are moderately small and subconical; in some specimens, the distal tubercle on the fourth finger is bifid. The supernumerary tubercles are distinct and conical. In most specimens, they are arranged in a single row on the proximal segments of each digit, but in some individuals the tubercles are crowded on the proximal segment of the second finger. A double palmar tubercle is present. A low, flat, elliptical tubercle is present on the prepollex, which is only moderately enlarged and in breeding males does not bear a horny nuptial excrescence. Webbing is lacking between the first and second fingers, and rudimentary between the others (fig. 55A). The legs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A thin, transverse dermal fold is present on the heel, and a distinct tarsal fold extends the full length of the tar-

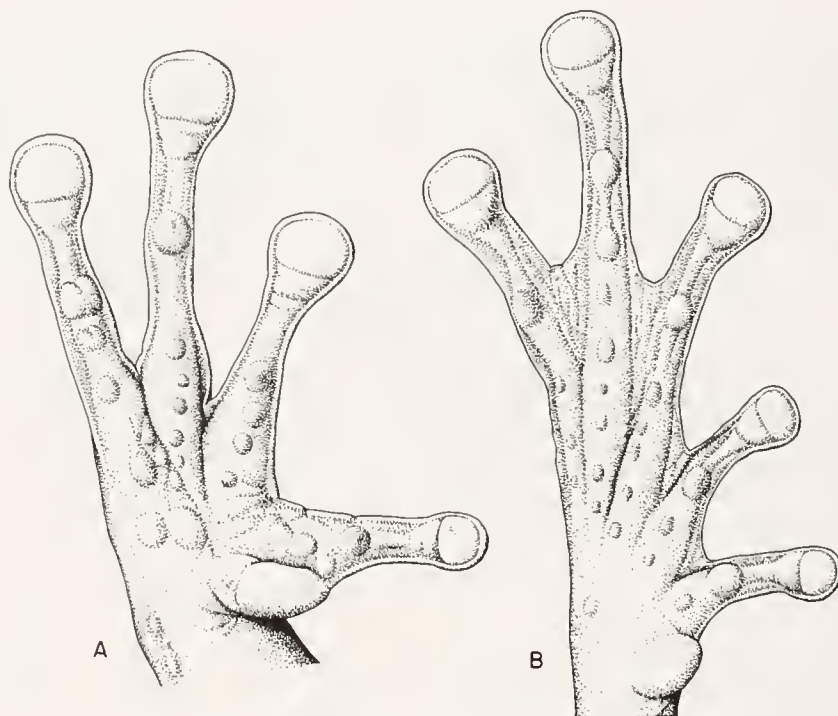


FIG. 55. Hand (A) and foot (B) of *Anothea spinosa* (K.U. No. 58075). $\times 3$.

sus. The inner metatarsal tubercle is moderately large, ovoid, and barely visible from above. A small, conical outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are small and conical, and the supernumerary tubercles are small, conical, and arranged in a single row on each digit. The toes are less than half webbed (fig. 55B). The webbing extends from the distal end of the antepenultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs. An elongate anal sheath is present; the anal opening is bordered on either side by a vertical dermal fold. The skin on the dorsum, exclusive

of the head, and the ventral surfaces of the limbs, except the thighs, is smooth; that on the throat, belly, and proximal posteroventral surfaces of the thighs is granular. In some specimens, small tubercles are present on the dorsal surfaces of the forearm. The tongue is broadly cordiform, shallowly notched behind, and barely free posteriorly. The dentigerous processes of the prevomers are relatively small, rounded elevations between the small, round choanae. There are five to 10 teeth on each process and a total of 10 to 19 prevomerine teeth; the average number of teeth in males is 12.6 and in females, 12.5. No vocal slits are evident in the specimens that I have examined; furthermore, I have not been able to ascertain the definite presence of a vocal sac.

The general coloration of *Anothea spinosa* is tan or brown above with dark brown or black on the side of the head and on the flanks (pl. 44, fig. 3). The dorsal ground color varies from pinkish tan to pale reddish brown or grayish brown. The tip of the snout and the ground color of the limbs is the same as the color on the dorsal surfaces of the head and body. A tan or pale gray vertical

bar is present on the lips anterior to the eye. Otherwise, the entire side of the head, the tympanum, and most of the axillary region are dark brown or black. Most of the venter, likewise, is dark brown or black; extensions of the dark ventral color are present on the flanks, usually as broad diagonal bars. The dorsal and posterior surfaces of the thighs, the ventral surfaces of the shanks, and the dorsal and ventral surfaces of the feet are marked with dark brown or black transverse bars. Black transverse markings are also present on the arms and on the fingers and toes. All of the black markings are narrowly outlined with white or pale creamy yellow. The iris is reddish bronze or coppery brown with or without fine black reticulations.

The coloration of juveniles resembles that of the adults, except that the limbs are more distinctly banded, especially ventrally, in the juveniles. The distinctive dark brown or black lateral markings, narrowly outlined by white are present, and the venter is dark brown.

In preservative, the dorsal ground color varies from dull reddish tan to dark gray. The lateral dark markings and the bands on the limbs are black, narrowly outlined by creamy white.

TADPOLES: The tadpoles of *Anotheca spinosa* were first described by Taylor (1954a). Starrett (1960a, p. 32) described some tadpoles which she thought to belong to *Anotheca spinosa* and questioned the identity of the tadpoles described by Taylor. Robinson (1961, p. 495) noted that on the basis of tadpoles collected in Veracruz, México, Taylor's tadpoles were correctly identified, whereas those described by Starrett did not belong to *Anotheca spinosa*. I have examined all of the tadpoles in question and have studied three additional lots of tadpoles, including young that were metamorphosed from these tadpoles. I concur with Robinson that the tadpoles that he and Taylor assigned to *Anotheca spinosa* are correctly identified, whereas those described by Starrett can not be assigned definitely to any known species of hylid.

A series of tadpoles in developmental stage 25 have body lengths of 6.8 to 8.8 (mean, 7.2) mm. and total lengths of 18.0 to 22.8 (mean, 19.7) mm.; a series of specimens in develop-

mental stage 33 have body lengths of 10.5 to 12.5 (mean, 11.7) mm. Four tadpoles in developmental stage 36 have body lengths of 13.7 to 16.0 (mean, 15.3) mm. The largest tadpole examined is in developmental stage 38 and has a body length of 17.1 mm. and a total length of 45.3 mm.

A typical tadpole in developmental stage 33 has a body length of 11.7 mm. and a total length of 27.5 mm. The body is moderately depressed and nearly flat above. The body is noticeably wider than deep and is widest posteriorly. In dorsal profile the snout is truncate, and in lateral profile it is rounded. The eyes are small, situated dorsally, and directed dorsolaterally. The nostrils are dorsal and situated about midway between the eyes and the tip of the snout. The spiracle is short and located ventrolaterally on the body; the spiracular opening is directed posteriorly at a point slightly more than midway between the snout and the posterior edge of the body. The anal tube is long. The caudal musculature is relatively heavy and extends to the tip of the rounded tail. The fins are fleshy and shallow; the ventral fin is slightly deeper than the dorsal fin (fig. 56).

In life the tadpoles are dark brown above and bluish gray below; the caudal musculature is brown, and the caudal fins are tan. In preservative, the entire tadpole is dull brown.

The mouth is anteroventral; its width is equal to about one-half of the greatest width of the body. The mouth is bordered by a single row of moderately large, blunt papillae. A faint lateral fold is present, and in this area a few small, blunt papillae are present. The beaks are immense and bear fine serrations. The upper beak extends laterally to the edges of the lip, and the ventral beak is broadly V-shaped. There are two upper and two lower rows of teeth. The second upper row is broadly interrupted medially. The teeth are relatively small and not continuous in the rows, especially the upper ones. All rows are about equal in length (fig. 57).

Tadpoles in developmental stage 25 have a nearly continuous first upper row of teeth and many teeth in the second upper row. Tadpoles in developmental stage 33 and later have a reduced number of teeth in the upper



FIG. 56. Tadpole of *Anotheca spinosa* (K.U. No. 60016). $\times 3$.

rows and show some reduction in the number of teeth in the lower rows.

MATING CALL: I have never observed *Anotheca spinosa* calling, nor have I traced an unknown call directly to an individual of this species. The apparent absence of vocal slits and a vocal sac possibly precludes the presence of a mating call in this species. However, I have heard an unknown frog call at Vista Hermosa, in northern Oaxaca, México, and the same call on the Río Changena, Bocas del Toro Province, Panamá. *Anotheca spinosa* is the only species of frog, whose voice I do not definitely know, that occurs at both of these localities. I provide a brief description of the call recorded at Vista Hermosa, in hope that a future worker might determine definitely whether or not this is the call of *Anotheca spinosa*.

One recording was obtained. The call consists of a series of notes, "boop-boop-boop," that are intensified in the latter part of the call. One hundred and seventy-eight notes were produced in 56 seconds. Each note has a duration of about 0.1 of a second and the interval between notes is about 0.3 of a second. The pulse rate is 220 pulses per second. The audiospectrogram (pl. 24, fig. 3), shows that the call is made up of four distinct harmonics. The lowest harmonic at about 540 cycles per second is the dominant frequency;

other harmonics are at about 1080, 1620, and 2160 cycles per second.

NATURAL HISTORY: *Anotheca spinosa* inhabits cloud forests, where apparently this species is active throughout the year. I have obtained adults in February, March, June, and August at Vista Hermosa, Oaxaca, México. Juveniles have been found in March and August.

Taylor (1954a) noted the egg eating habits of the tadpoles of this species. He obtained tadpoles from bromeliads at Moravia, Cartago Province, Costa Rica. Robinson (1961) found tadpoles of this species in a water-filled tree cavity on the south slopes of Volcán San Martín, Veracruz, México. I have also found tadpoles of this species on Volcán San Martín and in tree holes at Vista Hermosa, Oaxaca, México. Young tadpoles (developmental stage 25) contained mosquito larvae in the gut, whereas tadpoles in developmental stage 33 and later contained frog eggs in the gut. As noted by Taylor (1954a), the eggs contained in the gut do not seem to have been damaged in the process of ingestion. Some eggs in various early stages of development (up to gastrulation) were found undamaged in the gut of tadpoles. On the other hand, the mosquito larvae show evidence of having been chewed. Perhaps, the apparent change in diet from young to older developmental stages is correlated with the reduction of teeth in the later stages.

In one water-filled tree hole on the south slope of Volcán San Martín, the content of decomposing organic matter in the water resulted in a thick aqueous solution in which the tadpoles were living. In another cavity at Vista Hermosa, the amount of water was so slight that it was barely possible for all of the tadpoles to be completely submerged at one time. Evidently, the tadpoles of *Anotheca spinosa* are able to survive in water in which the oxygen content is extremely low.

At Moravia, Cartago Province, Costa Rica,

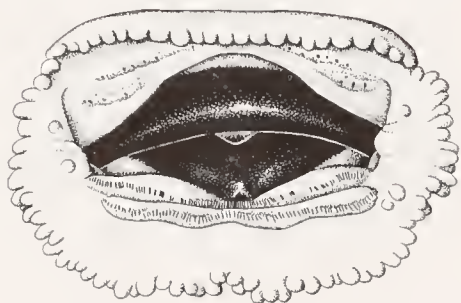


FIG. 57. Mouth of tadpole of *Anotheca spinosa* (K.U. No. 60016). $\times 17$.

where Taylor found the tadpoles of this species in bromeliads, it is possible that the tadpoles were feeding on eggs of another species of frogs. In Costa Rica, *Hyla zeteki* is known to lay eggs in bromeliads. At the Mexican localities where tadpoles of *Anotheca spinosa* have been found, I know of no other species of frog that deposits its eggs in tree holes, although *Hyla dendroscarta* lays its eggs in bromeliads. Perhaps, the tadpoles of *Anotheca spinosa* ingest eggs deposited by females of their own species. If this be true, the tadpoles are acting as a major control on the size of the population. Obviously, further study is needed on the ecology of this species.

Two young that were metamorphosed from tadpoles that were collected on Volcán San Martín, Veracruz, México, have snout-vent lengths of 15.9 and 19.7 mm.

REMARKS: Taylor (1954a, p. 594) commented on some minor differences between two Costa Rican specimens and several individuals from Veracruz, México. The differences that he noted between these populations, with regard to the cranial spines and ridges, apparently are the result of different degrees of development in different individuals and not populational differences. Although I have examined six specimens from Costa Rica and Panamá, I am unable to find any noteworthy differences between these individuals and the many specimens available from eastern México.

ETYMOLOGY: The specific name is Latin meaning thorny and refers to the spines on the dorsal periphery of the head.

DISTRIBUTION: *Anotheca spinosa* is known from elevations of 800 to 1800 meters on the Atlantic slopes of the Sierra Madre Oriental in Veracruz and northern Oaxaca, and in the Sierra de los Tuxtlas in southern Veracruz, México; this species also occurs at elevations from 300 to 1200 meters on the Caribbean slopes of Costa Rica and western Panamá, and one individual is known from El Valle on the Pacific slopes of Panamá (fig. 58).⁵

See Appendix 1 for the locality records of the 209 specimens examined.

⁵ Drs. Roy W. McDiarmid and Charles F. Walker have seen a photograph of an individual taken near San Vitio on the Pacific slopes of extreme eastern Puntarenas Province, Costa Rica.

Genus *Gastrotheca* Fitzinger

Gastrotheca Fitzinger, 1843, p. 30 [type species, *Hyla marsupiata* Duméril and Bibron, 1841, by monotypy].

Notodelphys Lichtenstein and Weinland, 1854, p. 373 [type species, *Notodelphys ovifera* Lichtenstein and Weinland, 1854; preoccupied by *Notodelphys* Allman 1847 (Crustacea)].

Nototrema Günther, 1859, p. 115 [replacement name for *Gastrotheca* Fitzinger, 1843].

Opisthodelphis Günther, 1859, p. 117 [substitute name for *Notodelphys* Lichtenstein and Weinland, 1854; preoccupied by *Notodelphys* Allman, 1847 (Crustacea)].

GENEROTYPE: The first usage of the generic name is in Fitzinger (1843, p. 30): "*Gastrotheca* . . . Am. . . . *Hyla marsupiata* Dum. & Bib." There is no other indication; thus, *Hyla marsupiata* Duméril and Bibron, 1841, is the type species of *Gastrotheca*.

ETYMOLOGY: The generic name is derived from the Greek *gastros*, meaning belly, and the Greek *theke*, meaning container, and refers to the brood pouch. Günther (1859, p. 115) noted Fitzinger's error of position and stated: "Fitzinger appears to have believed in the existence of a pouch on the belly; his denomination is derived from γαστήρ belly, and θήκη, used by the old anatomists for the brain-pan; therefore I think myself justified in not accepting his name." Günther proposed the name *Nototrema* (Greek *notos*, back) in reference to the dorsal brood pouch. Unfortunately, the Law of Priority necessitates the usage of the misleading name *Gastrotheca*.

DEFINITION: The following definition applies specifically only to those species inhabiting Middle America. These are large frogs with prominent heads. The head is casqued and the skin is co-ossified with the underlying dermal bones in one Central American species (*nicefori*) and several South American species (*angustifrons*, *weinlandi*, *fulvorufa*, and *ovifera*); in some other species (*ceratophrys* and *cornutum*) the skull is exostosed but co-ossification is absent. The webbing is reduced or absent on the hands, and the feet are no more than two-thirds webbed. The dorsum is unicolor brown, green, or gray or marked by darker longitudinal marks or transverse lines. The pupil is horizontal, and the palpebral membrane is clear. The vocal sac is single, median, and subgular; breeding males

FIG. 58. Distribution of *Anotheca spinosa*.

of some species have horny nuptial excrescences, whereas these are lacking in other species. Females have a dorsal brood pouch opening as a longitudinal slit posterior to the sacrum.

The skull of *Gastrotheca ceratophrys* is broader than long, deep, and well ossified (fig. 59). The frontoparietals are expanded laterally so as to form a flange over the orbit and part of the otic region; there is no frontoparietal fontanelle. The sphenethmoid is large and well ossified anteriorly so as to separate the nasals posteriorly. The nasals are well ossified laterally and in contact anteriorly. The maxillary process of the nasal is broadly sutured to the pars facialis of the maxillary; the two elements form a complete anterior margin for the orbit. The premaxillary is robust and has a long, slender alary process and a large palatine process. The maxillary is ro-

bust and has a high pars facialis. The squamosal is in broad bony contact with the crista parotica; the anterior arm of the squamosal is robust and articulates with the maxillary. The quadratojugal is robust and in bony contact with the maxillary. The prevomer is moderately developed; the anterior end lies dorsal to the pars dentalis of the maxillary. The dentigerous processes of the prevomers are small, posteromedially inclined, and widely separated medially. The palatine is moderately robust and has a ventral ridge. The pterygoid is robust and broadly articulated with the maxillary, prootic, and squamosal. Teeth are present on the premaxillaries, maxillaries, and prevomers but absent on the palatines and parasphenoid. All of the dermal roofing bones, the squamosal, and the pars facialis of the maxillary are exostosed.

Apparently in all species the eggs develop

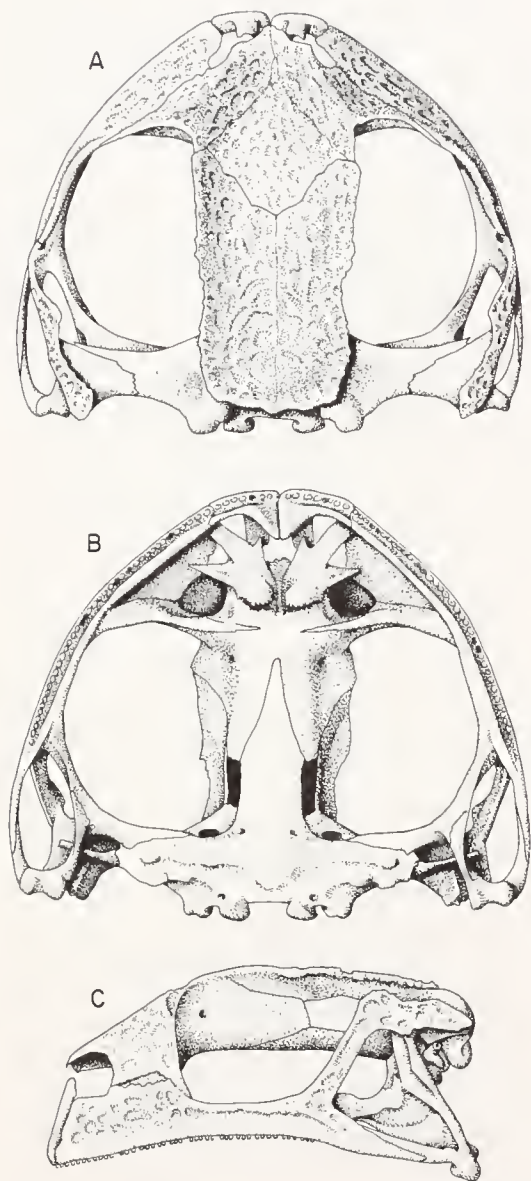


FIG. 59. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Gastrotheca ceratophrys*, K.U. No. 104361. $\times 2.5$.

in the brood pouch in the female. In *Gastrotheca marsupiatum* there is an aquatic larval stage, whereas in other species, in which the life history is known, an aquatic larval stage is absent; the eggs undergo direct development. The mating calls of the Central American species consist of a series of short notes (*ceratophrys*) or of a primary note followed

by a series of shorter secondaries (*nicefori*). The haploid number of chromosomes is 14 (known only in *G. ceratophrys*).

COMPOSITION OF GENUS: About nineteen species comprise the genus. The greatest diversity is in northwestern South America. Two species occur in lower Central America; of these, 14 preserved specimens and one skeleton have been examined.

ANALYSIS OF CHARACTERS: The two Central American species differ in a number of structural details, which are enumerated in the diagnoses. The feet of *Gastrotheca ceratophrys* have more webbing than do those of *nicefori* (fig. 60). The skin of the skull is co-ossified in *nicefori* and not in *ceratophrys*. The calls of the two species are noticeably different; that of *ceratophrys* consists of one to five short notes, and that of *nicefori* consists of a primary note followed by two to six secondary notes (pl. 36).

DISTRIBUTION: Southeastern highlands of Brazil, moderate to high elevations from Bolivia to Colombia and Venezuela, and low to moderate elevations in Panamá.

DISCUSSION: The two Central American species of *Gastrotheca* are members of two divergent species groups in South America. Currently all too little is known about the systematics of this interesting group of hylids. Three decades ago, Helen T. Gaige was actively working on these frogs; some 20 years ago, Charles F. Walker inherited the problem. Since then much new material has accumulated, but no synthesis of the group has appeared.

Gastrotheca ceratophrys (Stejneger)

Hyla ceratophrys Stejneger, 1911, p. 286 [holotype, U.S.N.M. No. 47705 from the upper Río Pequeni, Panamá Province, Panamá; A. H. Jennings collector].

Gastrotheca ceratophrys: Duellman, 1966b, p. 265 [transfer of *Hyla ceratophrys* Stejneger, 1911, to *Gastrotheca*].

DIAGNOSIS: This large species (males to 81 mm.) has long slender legs (tibiotarsal articulation extends well beyond the tip of the snout), thin transverse dermal ridges on the dorsum, triangular dermal flaps on the upper eyelids, skin on head not co-ossified, and the feet about two-thirds webbed. The other Central American *Gastrotheca* is smaller

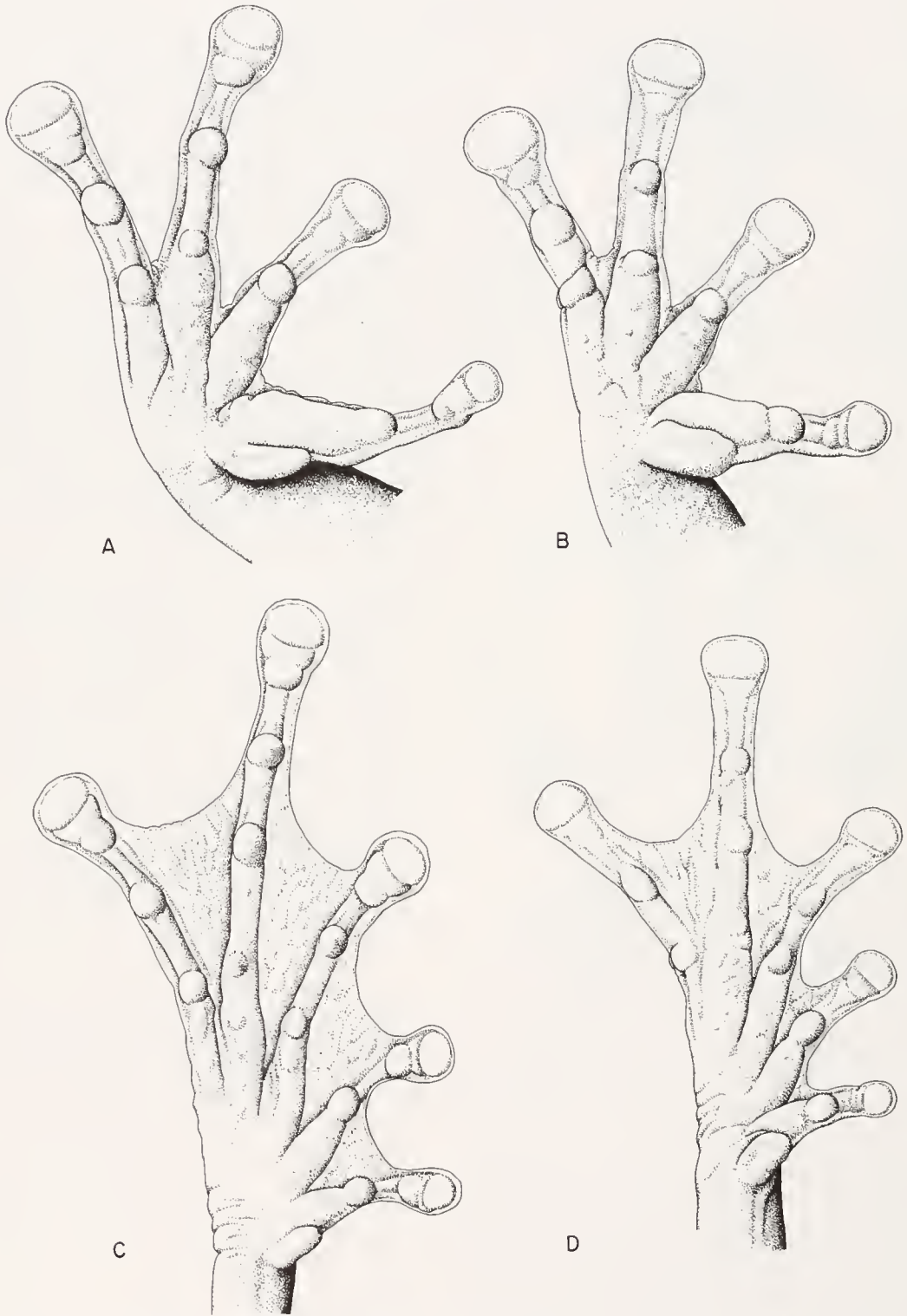


FIG. 60. Hands and feet of Middle American *Gastrotheca*. A and C. *G. ceratophrys*, K.U. No. 101535. B and D. *G. nicefori*, K.U. No. 111991. $\times 2.5$.

(males to 73 mm.) and has shorter legs (tibiotarsal articulation extends only to the eye), no transverse dermal folds on dorsum or triangular flaps on eyelids, skin of head co-ossified, and toes only half webbed. The only other Central American hylid having a triangular dermal flap on the upper eyelid is *Hemiphractus panamensis*, which has a triangular head, fleshy proboscis, neural processes protruding through skin on the dorsum, and virtually no webbing.

DESCRIPTION: Males of this large species attain a maximum known snout-vent length of 81.0 mm., and females reach 72.5 mm. In a series of four males from Panamá, the snout-vent length is 66.4 to 81.0 (mean, 74.2) mm.; the ratio of tibia length to snout-vent length is 0.561 to 0.615 (mean, 0.596); the ratio of foot length to snout-vent length is 0.447 to 0.464 (mean, 0.453); the ratio of head length to snout-vent length is 0.311 to 0.359 (mean, 0.338); the ratio of head width to snout-vent length is 0.348 to 0.386 (mean, 0.369), and the ratio of the diameter of the tympanum to that of the eye is 0.419 to 0.430 (mean, 0.426). One adult female having a snout-vent length of 72.5 mm. has a somewhat larger tympanum than that in males; the ratio of the diameter of the tympanum to that of the eye is 0.465.

The head is nearly as wide as the body, and the top of the head is slightly concave. In dorsal profile, the snout is bluntly rounded, and in lateral profile it is steeply inclined from the nostrils to the margins of the lips. The snout is rather short; the distance between the anterior corner of the eye and the nostril is about equal to the diameter of the eye. The nostrils are slightly protuberant at a point about three-fourths of the distance from the eyes to the anterior margin of the lips. The snout is high; the canthus is angular, and the loreal region is barely concave and inclined ventrolaterally. The lips are moderately thick and barely flared. A moderately large triangular dermal flap is present on the edge of the upper eyelid; in some individuals the flap is bifid terminally. A thin dermal fold extends posteriorly from the eye, above the tympanum, and posteriorly onto the sides of the body. The fold obscures the upper edge of the tympanum, which otherwise is barely discernible and separated from

the eye by a distance equal to about twice the diameter of the tympanum.

The arms are long and rather slender; an axillary membrane is absent. There is no row of tubercles on the ventrolateral edge of the forearm, nor is there a distinct transverse fold on the wrist. The fingers are long and slender and bear large discs; the width of the disc on the third finger is equal to half again the diameter of the tympanum. The subarticular tubercles are large and subconical; none is bifid. Supernumerary tubercles, when present on the hand, are barely evident on the proximal segments of the second and third fingers. No palmar tubercle, as such, is present. The prepollex is barely enlarged and in breeding males bears a diffuse horny, nuptial excrescence. The thumb is longer than the second finger, which is noticeably shorter than the fourth finger; webbing is lacking between the fingers (fig. 60A). The legs are long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends well beyond the tip of the snout. A transverse dermal fold is present on the heel, and in most individuals a small tubercle or calcar is evident on the heel. A weak, thin tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small and ovoid; no outer metatarsal tubercle is present. The toes are long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are large and round; small supernumerary tubercles are present on the proximal segments of the third, fourth, and fifth toes. The toes are about two-thirds webbed (fig. 60C). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. The opening is covered by a short, broad, anal sheath. A pair of large tubercles is present below the

anal opening. The skin on the dorsum is smooth, except for a few small pustules and a series of low, transverse ridges. There are eight to 12 ridges across the back, beginning on the head, anterior to the orbit. Usually the second, but sometimes the third, ridge crosses the eyelid. The skin on the dorsal surfaces of the limbs and the ventral surfaces of the shanks is smooth. The skin on the throat, belly, and ventral surfaces of the arms and thighs is granular, and the skin on the flanks is aerolate. Many small tubercles are present on the side of the head between the orbit and the tympanum. The opening of the brood pouch in the female is about midway between the sacral hump and the anal opening; the opening is puckered and triangular in shape. The tongue is broadly cordiform, shallowly notched behind, and not free posteriorly. The dentigerous processes of the prevomers are transverse or barely postero-medially inclined, medially separated, elevations between the moderately small, quadrangular choanae. There are seven to nine teeth on each process and a total of 14 to 18 (mean, 16.3) prevomerine teeth. No vocal slits are evident, but males have a single, median, subgular vocal sac that is moderately distensible.

The general coloration of *Gastrotheca ceratophrys* is tan or brown with darker, narrow transverse lines on the body and bars on the dorsal surfaces of the limbs (pl. 45, fig. 2). When active at night, these frogs usually are pale yellowish tan, grayish tan, or olive-tan. They have usually eight to 15 dark brown, narrow, transverse lines on the back and a somewhat wider dark brown dorsolateral stripe that begins on the supratympanic fold and extends to the groin. The dorsal surfaces of the limbs are colored like the body and are marked by numerous narrow transverse bars. There are five or six bars on the thigh, four or five on the shank, and three or four on the foot. The flanks and belly are creamy white. The anal region usually is dark brown, and the posterior surface of the thighs are pale brown. By day the frog usually becomes darker brown with still darker brown markings. The flanks change to creamy tan with brown venation. The throat is brown, and the belly and ventral

surfaces of the limbs are pinkish tan or pale brown. There are distinct vertical bars on the lip, which are most evident by day when they are dark brown and usually separated by a broad, conspicuous creamy white or pale yellow spot below the eye. There is a faint creamy yellow anal stripe. The webbing on the feet is brown. The iris is bronze peripherally and creamy yellow or olive-green medially. The palpebrum is clear.

In preservative the dorsum varies from tan to dull gray or dark brown with darker brown or nearly black transverse lines. The flanks usually are somewhat lighter and mottled or venated with brown. In those specimens killed by night, the venter is creamy white, whereas in those killed by day the venter is tan or dull brown. The posterior surfaces of the thighs varies from creamy tan to pale reddish brown. The white subocular spot is most evident in those individuals killed by day.

TADPOLES: The development of *Gastrotheca ceratophrys* is unknown. One female (K.U. No. 77016) contains nine eggs in the brood pouch. Each egg has a diameter of about 12 mm. and contains a small embryo having distinct eyes and a long tail bud (fig. 61). It is unknown whether these eggs would have developed into tadpoles, as in *Gastrotheca marsupiatum*, or if they would have developed directly into small frogs, such as is the case in most species of *Gastrotheca*. It is most likely that the aquatic larval stage is absent in this species.

MATING CALL: The call of *Gastrotheca ceratophrys* is a loud "bop." The call is reminiscent of the sound made from the pulling of a cork from a bottle of champagne. Frequently the call consists of a single note; other times two notes are given. One individual was heard to produce a single note followed by an interval of about one minute and then three notes in quick succession. Usually the interval between call groups is eight to 12 minutes. The duration of each note in one recording obtained is 0.08 of a second and the interval between the notes is 0.60 of a second. The notes consist of three harmonics at approximately 800, 1600, and 2400 cycles per second; the lowest harmonic is the domi-

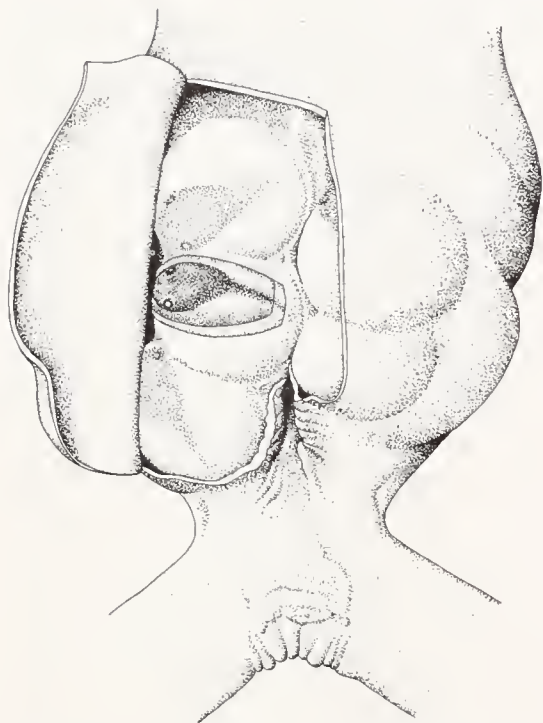


FIG. 61. Dorsal view of a female *Gastrotheca ceratophrys* (K.U. No. 77016) with the brood pouch opened on the left side to show the developing embryos, and the membranes removed from one egg. $\times 1.5$.

nant frequency. Each note noticeably diminishes in pitch (pl. 36, fig. 1).

NATURAL HISTORY: *Gastrotheca ceratophrys* inhabits tropical rain forest and low montane forest characterized by high humidity throughout the year. These large frogs are strictly nocturnal and arboreal. Individuals have been observed at heights of 12 meters above the ground, and the numerous voices from much greater heights indicate that this species is an inhabitant of the tree-tops in the tall forests. Calling males were heard at Almirante, Bocas del Toro Province, Panamá, on March 23, at the Río Changena and Río Claro, Bocas del Toro Province, in May, and at Laguna and Tacarcuna, Darién Province, in July. The single gravid female was obtained on July 5, 1963, at Laguna. Males characteristically call from branches or from vines between trees, high above the ground.

This has proved to be one of the most elusive frogs in lower Central America. Although an adult female was obtained at La-

guna in July, 1963, the voices, now known to belong to this species, were not associated with *Gastrotheca ceratophrys* at that time. Instead, we unsuccessfully searched for the "tree-top bopper" until a calling male was found near Almirante, on March 23, 1965. Although the characteristic loud voice of this frog belies its presence in a given area, the acquisition of specimens is extremely difficult. A week spent on the Río Changena in May, 1966, resulted in the collection of one specimen, although several males were heard calling from high elevations in the trees every night.

REMARKS: Cochran and Goin (1970) apparently overlooked Stejneger's name and description of *Hyla ceratophrys* and the fact that Duellman (1966b) placed this species in the genus *Gastrotheca*; they referred the specimen from Tacarcuna, Darién Province, Panamá (U.S.N.M. No. 141795), to *Gastrotheca cornutum* (Boulenger, 1898a). Another specimen (F.M.N.H. No. 54718) from the Río San Joaquín, Departamento Cauca, Colombia, was discussed at length by Cochran and Goin, who compared it with the holotype of *Gastrotheca cornutum* (B.M.N.H. No. 1947.2.22.-49) from Cachabe, Esmeraldas Province, Ecuador. Cochran and Goin noted that their Colombian specimen differed from the type of *cornutum* by having more webbing and by having definitive rows of tubercles arranged transversely on the back; furthermore, they noted some discrepancies in the coloration. A comparison of the Panamanian specimens with the description and illustration of *Gastrotheca cornutum* (Boulenger, 1898a, p. 124, pl. 18) confirms the differences noted by Cochran and Goin. It seems most likely that the specimen from Colombia is referable to *Gastrotheca ceratophrys*, which probably is a species distinct from, but closely related to, *Gastrotheca cornutum* in Ecuador.

ETYMOLOGY: The specific name is derived from the Greek *keras*, meaning horn, and the Greek *phryne*, meaning toad. The name, in reference to the dermal "horn" above the eye is used in the sense of the generic name for the large South American leptodactylids characterized by having a fleshy horn over each eye.

DISTRIBUTION: *Gastrotheca ceratophrys*

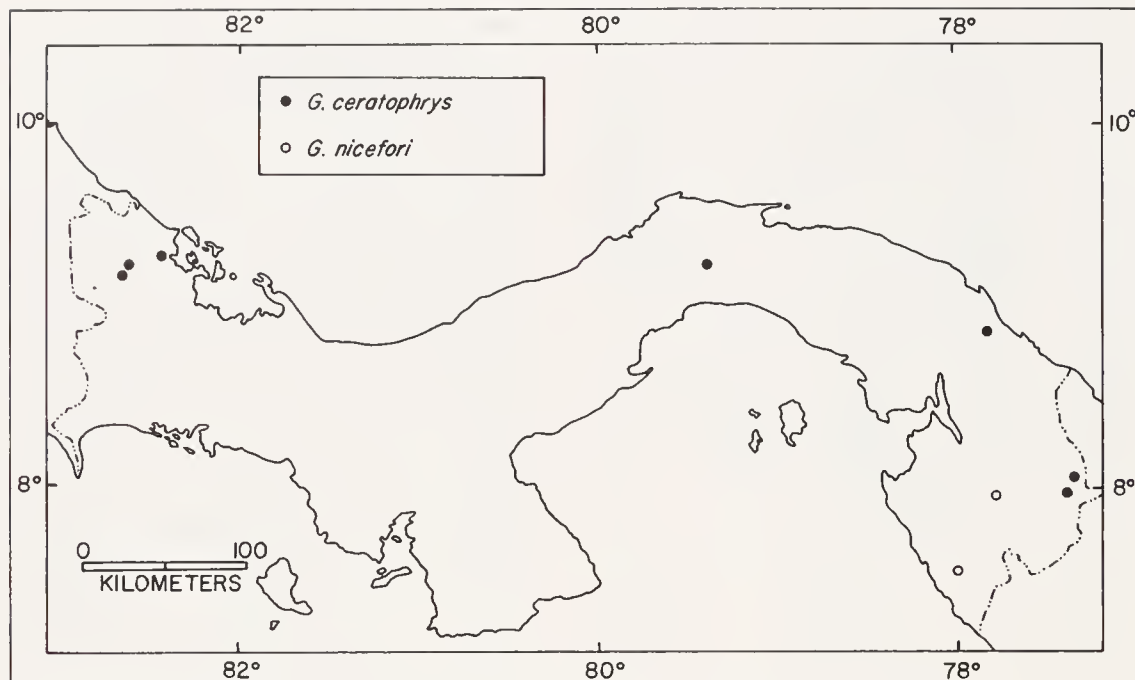


FIG. 62. Distribution of the Central American *Gastrotheca*.

occurs at elevations at less than 1500 meters on the Caribbean slopes in western and central Panamá and on the Pacific slopes in eastern Panamá and Colombia (fig. 62).

See Appendix 1 for the locality records of the 12 specimens examined.

Gastrotheca nicefori Gaige

Gastrotheca nicefori Gaige, 1933, p. 1 [holotype, U.M.M.Z. No. 73242 from Pensilvania, Departamento Caldas, Colombia; Hermano Nicéforo Mariá collector].

DIAGNOSIS: This moderately large species (males to 73 mm.) has short legs (tibiotarsal articulation extends to the eye), the skin of the head co-ossified and the feet about half webbed. The other Central American species, *G. ceratophrys*, lacks co-ossification, is larger (males to 81 mm.), and has the feet two-thirds webbed and the tibiotarsal articulation extends well beyond the tip of the snout; furthermore, *ceratophrys* has transverse dermal folds on the dorsum and triangular dermal flaps on the upper eyelids. Other casque-headed Middle American hylids differ by having spines on the head (*Anotheca*), broad labial shelves and a prenasal bone (*Tripiron*),

or a spatulate snout and spade-like inner metatarsal tubercles (*Pternohylla*).

DESCRIPTION: Males of this moderately large species attain a maximum snout-vent length of 73.5 mm., and females reach 82.0 mm. In a series of three males from Darién Province, Panamá, the snout-vent length is 58.8 to 73.5 (mean, 66.6) mm.; the ratio of tibia length to snout-vent length is 0.490 to 0.522 (mean, 0.508); the ratio of foot length to snout-vent length is 0.433 to 0.479 (mean, 0.460); the ratio of head length to snout-vent length is 0.331 to 0.352 (mean, 0.340); the ratio of head width to snout-vent length is 0.371 to 0.395 (mean, 0.381), and the ratio of the diameter of the tympanum to that of the eye is 0.474 to 0.569 (mean, 0.507). No females are available from Central America.

The head is as wide as the body, and the top of the head is concave. The skin is co-ossified with the underlying cranial elements; a distinct, but low transverse occipital ridge is evident, and a lateral bony supratympanic ridge is present. In dorsal profile, the snout is bluntly rounded; in lateral profile, the snout is abruptly inclined from the nostril to the

margin of the lip. The snout is moderately short; the distance from the anterior corner of the eye to the nostril is slightly greater than the diameter of the eye. The nostrils are barely protuberant at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is angular, and the loreal region is concave and inclined laterally to the moderately thin, slightly flared lips. A bony ridge extends posteriorly from the eye above the tympanum, and posterior to the ridge a dermal fold continues onto the side of the body. The upper edge of the tympanum is obscured by the tympanic crest; otherwise, the tympanum is distinct and separated from the eye by a distance equal to half again the diameter of the tympanum. The arms are long and moderately robust; an axillary membrane is absent. The forearms are devoid of a row of tubercles, but a distinct dermal fold is present on the wrist. The fingers are moderately long and robust and bear large discs; the width of the disc on the third finger is equal to half again the diameter of the eye. The subarticular tubercles are large and round; none is bifid. Small, conical supernumerary tubercles are present on the proximal segments of the second, third, and fourth fingers. No distinct palmar tubercle is evident. The prepollex is moderately enlarged and in breeding males bears a faint nuptial excrescence. The thumb is longer than the second finger, which is noticeably shorter than the fourth. Webbing is lacking between the first and second fingers, whereas the other fingers are barely webbed basally (fig. 60B). The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the eye. A thin transverse dermal fold is present on the heel, but tubercles and a calcar are absent. The inner metatarsal tubercle is low, flat, and elliptical. No distinct outer metatarsal tubercle is present. The toes are long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are moderately large and round; faint supernumerary tubercles are present on the proximal segments of each digit. The toes are about half webbed (fig. 60D). The webbing connects the first and

second toes at the level of the distal end of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and from the middle of the antepenultimate phalanx of the fourth to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs; it is covered by a short, narrow anal sheath and bordered below by two moderately large tubercles. The skin on the dorsum is aerolate, and that on the head is co-ossified. The skin on the throat, belly, and ventral surfaces of the thighs is granular; elsewhere, the skin on the venter is smooth. The tongue is nearly round, barely notched posteriorly, and not free behind. The dentigerous processes of the prevomers are small, narrowly separated elevations between the small round choanae. The three males have six to eight teeth on each process and a total of 13 to 16 (mean, 14.3) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Gastrotheca nicefori* consists of a tan or pale grayish brown dorsum with dark brown flanks and concealed surfaces of the limbs (pl. 45, fig. 1). The following descriptions of coloration are taken from the field notes of Charles W. Myers.

K.U. No. 101538—By day all exposed dorsal surfaces were silvery gray with white and a few brownish spots sparsely and irregularly scattered on the dorsum. An ill-defined bronze stripe extends from the eye to the arm and barely includes the tympanum in its width. A pale pink line extends from above the tympanum to the groin. Extensive areas of dark blue are present in the axilla, on the undersides of the arms, on the posterior part of the flank into the groin, and onto the anterior surface of the thigh, on the posterior surface of the thigh, the ventral surface of the shank, and on to the inner side of the top of the foot, and on the webs of the hand and feet. In addition, the anterior part of the flank bears dark striations. The throat and adjacent

part of the chest is silvery gray becoming darker gray over the rest of the ventral surfaces. The iris is pale gray. After dark the specimen became brown above, and the white spots and pink line became pale brown, whereas this brown spot that had been present by day became blackish brown. The iris changed to pale grayish brown. The ventral surfaces also darkened.

K.U. No. 101539—The dorsum is yellowish brown with a few blackish brown spots. An indefinite yellow line separates the dorsal color from the darker color on the flanks. The flanks and concealed surfaces of the limbs and venter are dark brown, darkest on the flanks and posterior surfaces of the thighs. No blue color was observed. The iris is pale brown. This specimen did not exhibit metachrosis.

K.U. No. 111991—The dorsum was pale grayish brown at night and changed to a medium brown by day. The flanks, groin, and anterior and posterior surfaces of the thighs are dark brown, almost black on the thighs, with a few small touches of pink on the flanks and a barest tinge of blue on the posterior surfaces of the thighs. The venter is pale dirty grayish brown. The iris is pale grayish brown with very fine black reticulations.

In preservative, the dorsum is grayish tan with scattered small brown spots on the back and dorsal surfaces of the limbs. The flanks and anterior and posterior surfaces of the thighs are dark brown. The venter is dull grayish brown.

TADPOLES: The early development of *Gastrotheca nicefori* is unknown; presumably, the species undergoes direct development and aquatic larvae are absent.

MATING CALL: The call of *Gastrotheca nicefori* consists of a series of chicken-like "clucks." The call consists of a moderately long primary note and two to six shorter secondary notes. In one recording, three call groups were emitted in a period of eight seconds, followed by a 12 second interval and one more call group. The duration of the primary note varies from 0.5 to 0.6 of a second and of the secondaries from 0.15 to 0.20 of a second. There are 80 to 90 pulses per second; the fundamental frequency is at approximately 87 cycles per second, and the

dominant frequency is at about 957 cycles per second (pl. 36, fig. 2).

NATURAL HISTORY: The limited information on the ecology of this species has been gleaned from the field notes of Charles W. Myers, who collected the only Central American specimens. He obtained two specimens from cloud forests on Cerro Cituro in the Serranía de Pirre, Darién Province, Panamá, in January, 1966. Both were found at night; one was on a vine-covered stump, and the other one was calling from a bromeliad-choked limb of a tree about 12 meters above the ground. Another individual was found about five meters above the ground at night in the Serranía del Sapo on April 23, 1967.

REMARKS: Two of the Panamanian specimens were compared with the holotype of *Gastrotheca nicefori* by Charles F. Walker and myself; no distinctive structural differences could be found. The holotype is badly faded so that color comparisons were meaningless.

It is interesting to note that in Panamá, this species is known only from the Serranía del Sapo and the Serranía de Pirre, whereas *Gastrotheca ceratophrys* occurs in the Cordillera de San Blas and Serranía del Darién in eastern Panamá. Thus, on the basis of very limited data the geographic ranges of the two species seem to be complementary; furthermore, *G. ceratophrys* apparently occurs at elevations notably lower than those at which *nicefori* is found.

ETYMOLOGY: The specific name is a patronym for Hermano Nicéforo María, who has contributed so much to our knowledge of Colombian herpetology.

DISTRIBUTION: *Gastrotheca nicefori* occurs at elevations between 800 and 1100 meters in the Serranía de Pirre and Serranía del Sapo in extreme eastern Panamá and at these and higher elevations in the Andes of central Colombia (fig. 62).

See Appendix 1 for the locality records of the three specimens examined.

Genus *Phrynohyas* Fitzinger

Phrynohyas Fitzinger, 1843, p. 30 [type species, *Hyla zonata* Spix, 1824 (= *Rana venulosa* Laurenti, 1768) by monotypy and declaration of the International Commission on Zoological Nomenclature (Opinion No. 520, 1958)].

Acrodytes Fitzinger, 1843, p. 30 [type species, *Hyla venulosa* Daudin, 1803 (= *Rana venulosa* Laurenti, 1768) by monotypy; generic name suppressed by the International Commission on Zoological Nomenclature (Opinion No. 520, 1958) for purposes of the Law of Priority, but not for those of the Law of Homonymy].

Scytotis Cope, 1862 [type species, *Scytotis hebes* Cope, 1862, by monotypy].

GENEROTYPE: The determination of the status of the names applicable to the frogs in this genus has been one of the most chaotic cases of nomenclatural confusion in herpetology. Duellman (1956a) considered that the frogs previously referred to *Hyla venulosa* were generically separate from *Hyla* and presented evidence that the correct generic name was *Phrynohyas*. The problem originated with Fitzinger's (1843, p. 30) cryptic generic assignments:

"*Phrynohyas*

Cephalophractus Fitz.—*Cephalo-*

galeatus Fitz.

Trachycephalus Tschud.—*Trachy-*

nigromaculatus Tschud.

Phrynohyas—*Hyla zonata* Spix

Acrodytes—*Hyla venulosa* Daudin"

As discussed by Duellman (1956a, p. 7), *Cephalophractus* and *C. galeatus* are *nomina nuda*. *Trachycephalus* is a valid genus containing three species (Trueb, 1970a, 1970b). Duellman (1956a, p. 7) argued that *Acrodytes* and *Hyla venulosa* were *nomina dubita*: "It is evident from the examination of Fitzinger's work that the person's name following each specific name is usually the authority for the current generic and specific word combination, rather than the original describer of the species. Thus, since Daudin first used the combination *Hyla venulosa*, his name appears after the specific name instead of that of the original describer of *venulosa*, namely Laurenti. Although Daudin, both in 1802 when he referred *venulosa* to the genus *Rana* and in 1803 when he referred it to *Hyla*, described and figured (1802) a hylid frog with paired lateral vocal sacs behind the angles of the jaws, he considered the specific name as that of Laurenti (1768). Laurenti based his description on a plate in Seba (1734, I:115, pl. 72, fig. 4). This figure cannot, by any exercise of the imagination, conceivably be that of a hylid frog. There are no webs or toe

discs; furthermore, there is a dorsolateral fold! Daudin was in error, therefore, when he used Laurenti's name *venulosa* for a hylid frog with paired lateral vocal sacs. Unfortunately, this error has been perpetuated through the literature for the past 150 years. Since the name *Rana venulosa* Laurenti cannot be applied to any hylid frog, and since neither the figure nor the description gives any possible clues to the identity of the frog figured by Seba, the name *Rana venulosa* must be considered a *nomen dubium*. It follows that the generic name *Acrodytes* (with *Rana venulosa* Laurenti [= *Hyla venulosa* Daudin] the type species by monotypy) also must be considered a *nomen dubium*. Thus, *Phrynohyas* (type species *Hyla zonata* Spix by monotypy) is the correct generic name for those hylid frogs with paired lateral vocal sacs behind the angles of the jaws and without the skin of the head co-ossified with the skull."

Duellman (1956b, p. 145) requested that the International Commission on Zoological Nomenclature suppress the generic name *Acrodytes* Fitzinger, 1843, and the specific name *venulosa* Laurenti, 1768, for the purposes of the Law of Priority but not for those of the Law of Homonymy, and to place *Phrynohyas* Fitzinger, 1843 (type species, by monotypy: *Hyla zonata* Spix, 1824) on the Official List of Generic Names in Zoology. Skillful legal manipulation by the commission resulted in *Acrodytes* being suppressed and *Phrynohyas* being placed on the Official List of Generic Names in Zoology with "*Rana venulosa* Laurenti, 1768 (= *Hyla zonata* Spix, 1824)" as the type species (see Hemming, 1958). This action served to conserve the well-known specific name *venulosa*.

Duellman (1956a, p. 8) considered *Hyla tibiatrix* Laurenti, 1768, a name usually placed in the synonymy of *venulosa*, to be a *nomen dubium* and (1956b, p. 145) requested the suppression of the specific name, a request that was acted upon favorably by the International Commission on Zoological Nomenclature (Opinion No. 520) (Hemming, 1958). Rivero (1961) was unaware of this opinion when he suggested that Duellman's treatment of *venulosa* as a *nomen dubium* be followed but that *Hyla tibiatrix* be used instead of *Phrynohyas zonata*.

Thus, after all of these decades of confusion, the ruling by the International Commission on Zoological Nomenclature (Opinion No. 520) should result in nomenclatural stability with *Rana venulosa* Laurenti, 1768, as the type species of *Phrynohyas* Fitzinger, 1843.

ETYMOLOGY: The generic name is derived from the Greek *phrynos*, meaning toad, and *Hylas*, a character in Greek mythology. The generic name literally means a toad-tree frog.

DEFINITION: The frogs in this genus are large pond-breeding species; males attain snout-vent lengths of 100 mm. and females, 114 mm. The dorsum is tan or brown usually with a darker blotch or two on the back and transverse marks on the limbs. The fingers are about one-third and the toes about two-thirds webbed. Dermal appendages and an axillary membrane are absent. The palpebral membrane is clear. The skin on the dorsum is thick, glandular, and pustulate; there is no integumentary-cranial co-ossification. Males have paired lateral vocal sacs behind the angles of the jaws and horny nuptial excrescences on the prepollices. The skull is broad and well ossified; there is no frontoparietal fontanelle (fig. 63). The maxillaries and premaxillaries are robust. The nasals are large, in broad contact medially, and broadly sutured with the sphenethmoid, which is well ossified. The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosals is in bony contact with the crista parotica; the anterior arm of the squamosal extends about half of the distance to the maxillary. A quadratojugal is present and articulates with the maxillary. The prevomers are large; their dentigerous processes are massive and curved. The medial ramus of the pterygoid is in bony contact with the prootic. Bifid, spatulate teeth are present on the maxillaries, premaxillaries, and prevomers. The tadpoles have deep caudal fins, a median anal tube and anteroventral mouths with four upper and six lower rows of teeth. The mating call consists of a loud series of growls. The haploid number of chromosomes is 12.

COMPOSITION OF THE GENUS: The number of species in this genus is unknown at this time. The only Middle American species, *P. venulosa*, is widespread in South America;

perhaps *P. hebes* (Cope) is conspecific with *venulosa*. Other South American species include *P. mesophaea* (Hensel) and *P. imitatrix* (Miranda-Ribeiro) in eastern Brazil, *P. ingens* Duellman in the Maracaibo Basin, *P. macrotis* in Amazonian Ecuador, and *P. coriacea* (Peters) in the Amazon Basin and Guianas. I have examined 775 preserved frogs, seven skeletons, and four lots of tadpoles of *P. venulosa* from Middle America.

DISTRIBUTION: The genus occurs throughout subhumid lowlands from central Tamaulipas and southern Sinaloa, México, southward through Middle America (Pacific lowlands only in lower Central America) to South America, where it is widespread east of the Andes southward to northern Argentina.

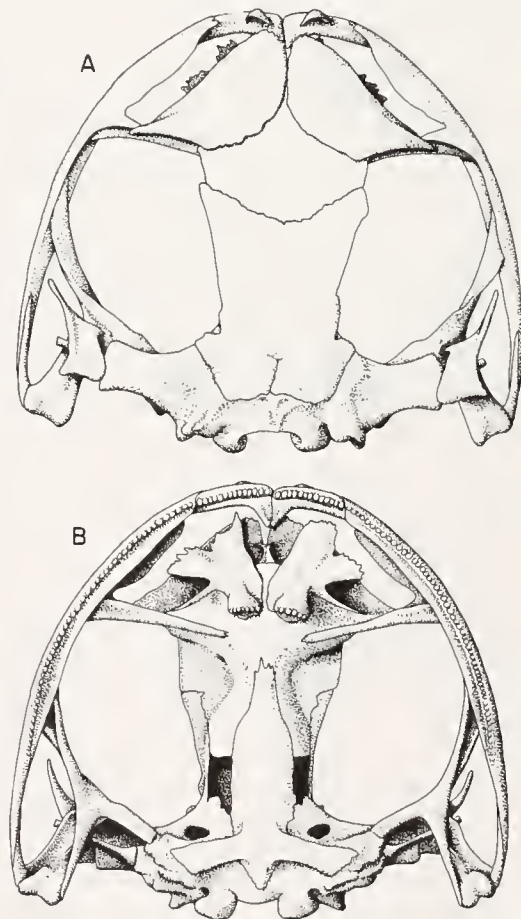


FIG. 63. Dorsal (A) and ventral (B) views of the skull of *Phrynohyas venulosa*, K.U. No. 68175. $\times 3$.

DISCUSSION: The greatest amount of differentiation in *Phrynohyas* is in South America. Duellman (1956a) recognized five species in Middle America, but these are currently considered to be nothing more than variants of the widespread *Phrynohyas venulosa* (Duellman, 1966b, and McDiarmid, 1968).

Two of the currently recognized species in South America apparently are closely related to *P. venulosa*. One of these, *P. hebes* of Paraguay, northern Argentina, and southern Minas Geras, Brasil, possibly is conspecific with *venulosa*, whereas the other, *P. ingens*, occurs sympatrically with *venulosa* in the Maracaibo Basin of Venezuela and Colombia (Cochran and Goin, 1970). *Phrynohyas imitatrix* and *mesophaea* are much smaller than *venulosa* and occur in south-eastern Brasil. *Phrynohyas coriacea* is known from the Guianas and the upper Amazon Basin; it also is smaller and more brightly colored than *venulosa* (Duellman, 1968c).

Only four currently recognized genera of hylids have paired lateral vocal sacs behind the angles of the jaws. There are *Phrynohyas*, *Argenteohyla*, *Osteocephalus*, and *Trachycephalus*. The last genus is characterized by extensive integumentary-cranial co-ossification and the development of a cranial casque. Trueb (1970a) noted that the differences between the skulls of *Osteocephalus* and *Trachycephalus* are principally the result of a marked evolutionary trend toward increased dermal ossification from the former to the latter. Furthermore, she suggested that on the basis of cranial morphology, *Phrynohyas* "represents a logical choice for the modern descendent of a progenitor which gave rise to a single phyletic line of casque-headed frogs beginning with *Osteocephalus* and terminating with *Trachycephalus jordani*."

Phrynohyas venulosa Laurenti

Rana venulosa Laurenti, 1768, p. 31 [based on a plate in Seba (1734, vol. 1, pl. 72, fig. 4)].

Hyla venulosa: Daudin, 1803, p. 71. Boulenger, 1882a, p. 364. Günther, 1901 (1885-1902), p. 272. Kellogg, 1932, p. 154.

Hyla zonata Spix, 1824, p. 41 [type unknown; from Lago Tefé at mouth of Rio Tefé, Amazonas, Brasil; collector unknown].

Hyla bufonia Spix, 1824, p. 42 [type unknown; from Eca, Amazonas, Brasil; collector unknown].

Hyla vermiculata Duméril and Bibron, 1841, p. 563 [holotype, M.N.H.N. No. 4797 from "Amerique"; presented by Mr. Harlan].

Phrynohyas zonata: Fitzinger, 1843, p. 30. Duellman, 1956a, p. 35.

Acrotytes venulosa: Fitzinger, 1843, p. 30. Taylor, 1944b, p. 64; 1952c, p. 800.

Hyla lichenosa Günther, 1859 [lectotype, B.M.N.H. No. 1936.12.3.119 from Amazonas, Brasil; collector unknown]. Brocchi, 1882, p. 33. Boulenger, 1882a, p. 364.

Scytotis venulosus: Cope, 1866b, p. 85.

Hyla spilomma Cope, 1877, p. 86 [holotype, apparently lost, from Cosamaloapam, Veraacruz, México; Francis Sumichrast collector]. Brocchi, 1881, p. 39. Günther, 1901 (1885-1902), p. 282.

Hyla paenulata Brocchi, 1879, p. 21 [holotype, formerly in M.N.H.N., now lost, from western (southern) Guatemala; collector unknown]; 1882, p. 45.

Hyla nigropunctata Boulenger, 1882a, p. 366 [syn-types, B.M.N.H. Nos. 59.9.20.2 and 81.10.31.20 from Jalapa, Veracruz, México; Mr. Hoege collector].

Hyla resinifetrix Goeldi, 1907, p. 135 [holotype, B.M.N.H. No. 1947.2.23.24 from San Antonio do Prata, Pará, Brasil; Emil Goeldi collector].

Acrotytes inflata Taylor, 1944b, p. 63 [holotype, F.M.N.H. No. 100046 (formerly E.H.T.-H.M.S. No. 17890) from La Venta, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 74.

Acrotytes spilomma: Taylor, 1944b, p. 64. Smith and Taylor, 1948, p. 75.

Acrotytes modesta Taylor and Smith, 1945, p. 594 [holotype, U.S.N.M. No. 115013 from Cruz de Piedra, near Acacoyagua, Chiapas, México; Hobart M. Smith collector]. Smith and Taylor, 1948, p. 74.

Phrynohyas inflata: Duellman, 1956a, p. 19.

Phrynohyas latifasciata Duellman, 1956a, p. 24 [holotype, B.M.N.H. No. 83.2.7.1 from Presidio, Sinaloa, México; Alphonso Forrer collector].

Phrynohyas modesta: Duellman, 1956a, p. 25. Stuart, 1963, p. 37.

Phrynohyas spilomma: Duellman, 1956a, p. 28. Stuart, 1963, p. 37.

Phrynohyas corasterias Shannon and Humphrey, 1957, p. 15 [holotype, U.I.M.N.H. 67060 (formerly F.A.S. No. 11307) from 4.8 miles east of San Blas, Nayarit, México; Frances L. Humphrey and Frederick A. Shannon collectors].

Phrynohyas venulosa: Henning, 1958, p. 172. McDiarmid, 1968, p. 2.

Hyla tibiatrix tibiatrix: Rivero, 1961, p. 127.

Hyla venulosa venulosa: Rivero, 1964, p. 311.

DIAGNOSIS: This large tree frog has thick glandular skin on the dorsum and heavily granular skin on the venter. Most individuals

have a dark dorsal blotch, which is continuous from the occiput to the posterior end of the body, transversely interrupted in the sacral region, or medially divided anteriorly. Distinct transverse bands are present on the limbs. Some individuals are unicolor brown above. *Phrynohyas venulosa* differs from all other Middle American hylids by having paired lateral vocal sacs behind the angles of the jaws and by having thick glandular skin on the dorsum. *Phrynohyas* lacks the vertical bars on the lips and cream and black mottling on the flanks characteristic of *Smilisca baudinii*, the only other Middle American species easily confused with *Phrynohyas*.

DESCRIPTION: Males of this large species attain a maximum known snout-vent length of 100.5 mm., and females reach 113.7 mm. In a series of 23 males from 4 kilometers west-northwest of Esparta, Puntarenas Province, Costa Rica, the snout-vent length is 79.9 to 95.6 (mean, 88.6) mm.; the ratio of tibia length to snout-vent length is 0.436 to 0.484 (mean, 0.461); the ratio of foot length to snout-vent length is 0.374 to 0.419 (mean, 0.394); the ratio of head length to snout-vent length is 0.264 to 0.299 (mean, 0.284); the ratio of head width to snout-vent length is 0.306 to 0.346 (mean, 0.330), and the ratio of the diameter of the tympanum to that of the eye is 0.539 to 0.794 (mean, 0.682). Four females from the same locality have snout-vent lengths of 92.6 to 105.9 (mean, 98.1) mm. They differ from the males by having slightly larger tympani; the ratio of the diameter of the tympanum to that of the eye is 0.635 to 0.766 (mean, 0.715). McDiarmid (1968) in a careful analysis of variation in this species in Middle America, showed that the largest individuals are found in northwestern México and in southern Costa Rica and Panamá. My data, based in a large part on the examination of the same specimens as studied by McDiarmid, support these conclusions. Fourteen males from 10 kilometers west-southwest of Chepo, Panamá Province, Panamá, have snout-vent lengths of 77.8 to 99.8 (mean, 88.0) mm., and three females from the same locality have snout-vent lengths of 97.8 to 106.4 (mean, 102.8) mm. The largest specimens from Middle America are from Palmar, Puntarenas Province, Costa Rica; five males have

snout-vent lengths of 92.7 to 100.5 (mean, 95.8) mm., and three females have snout-vent lengths of 96.6 to 113.7 (mean, 104.4) mm. (table 14). Although there is considerable variation in proportions in series of specimens from throughout the range of this species in Middle America, there are no statistically significant differences.

The head is somewhat narrower than the body, which is robust; the top of the head is flat. In dorsal profile, the snout is bluntly rounded; in lateral profile it is bluntly round or nearly truncate. The snout is moderately short; the nostrils are noticeably protuberant at a point about four-fifths of the distance from the eyes to the tip of the snout. The internarial region is slightly depressed. The canthus is rounded, but distinct; the loreal region is barely concave and the lips are moderately thin and flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. In some specimens, the fold is excessively heavy and nearly completely obscures the tympanum. In others, only the upper edge of the tympanum is obscured; otherwise, the tympanum is distinct and separated from the eye by a distance equal to the diameter of the tympanum.

The arms are short and robust; an axillary membrane is absent. No distinct row of tubercles is present on the ventrolateral edge of the forearm, but a heavy dermal fold is present on the wrist. The fingers are short and robust and bear large discs; the width of the disc on the third finger is greater than the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercles on the fourth finger is bifid in most specimens. The supernumerary tubercles are small and indistinct. No distinct palmar tubercle is evident. The prepollex is moderately enlarged and in breeding males bears a smooth, horny nuptial excrescence. The fingers are about one-half webbed (fig. 64A). The webbing is vestigial between the first and second fingers and extends from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, and from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth

TABLE 14
Geographic Variation in Snout-vent Length,
With Means in Parentheses, of *Phrynohyas venulosa*.

Locality	N	Males Size	N	Females Size
Sinaloa, México ^a	6	74.2-90.2 (80.9)	1	89.0
Nayarit, México	15	79.8-91.2 (85.3)	1	97.3
Colima-Guerrero, México	5	63.5-92.0 (80.3)	0
Tamaulipas, México	2	72.0-80.0 (76.0)	3	74.0-77.0 (75.0)
San Luis Potosí, Mexico	4	74.0-86.0 (81.0)	7	63.0-84.0 (69.4)
Veracruz, México	68	57.0-78.0 (66.4)	60	56.0-77.0 (66.1)
Yucatan Peninsula	10	73.0-87.0 (78.4)	4	71.0-92.5 (81.4)
El Petén, Guatemala	21	60.0-82.0 (72.7)	9	73.0-82.0 (76.7)
Pacific Chiapas	13	54.0-69.5 (63.7)	14	52.0-80.5 (63.5)
Pacific Guatemala	52	55.1-72.3 (64.1)	20	61.1-80.2 (65.2)
Esparta, Costa Rica	23	79.9-95.6 (88.6)	4	92.6-105.9 (98.1)
Palmar, Costa Rica	5	92.7-100.5 (95.8)	3	96.6-113.7 (104.4)
Chepo, Panamá	14	77.8-99.8 (88.0)	3	97.8-106.4 (102.8)

^a Data from McDiarmid (1968.)

finger. The legs are short and robust. In adults, the heels of the adpressed limbs overlap by about one-sixth of the length of the shank; the tibiotarsal articulation extends to the point of insertion of the arm. A heavy transverse dermal fold is present on the heel, and a distinct, curved, tarsal fold is present. The inner metatarsal tubercle is large and ovoid; a small conical outer metatarsal tubercle is present. The toes are moderately short and bear discs that are noticeably smaller than those on the fingers. The sub-articular tubercles are moderately large and subconical; the supernumerary tubercles are small and numerous on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 64B). The webbing extends from the base of the disc of the first toe to

the base of the penultimate phalanx of the second, from the base of the disc of the second to the distal end of the antepenultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs; a short anal sheath is present. The skin on the dorsum is smooth or weakly tuberculate in adults and heavily tuberculate in small individuals. The skin on the throat, belly, and postero-ventral surfaces of the thighs is heavily granular, and that on the other ventral surfaces is smooth. The tongue is broadly cordiform, deeply notched posteriorly, and barely free behind. The dentigerous processes of the

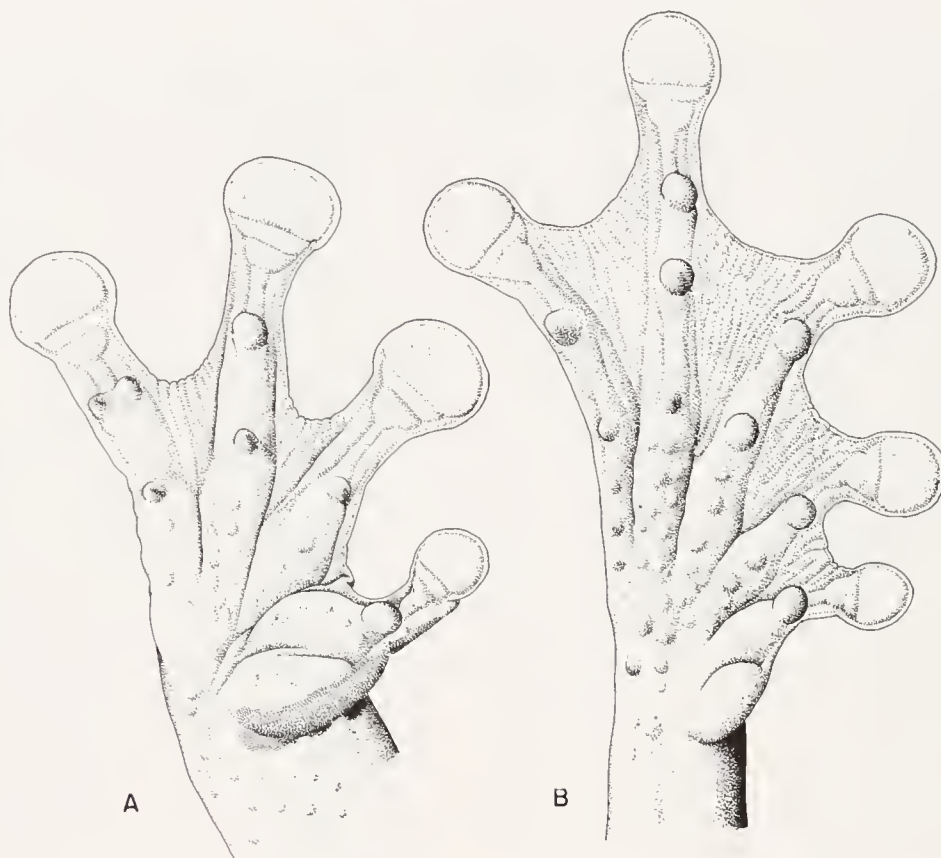


FIG. 64. Hand (A) and foot (B) of *Phrynohyas venulosa*, K.U. No. 108867. $\times 2.5$.

prevomers are slightly curved, transverse, narrowly separated elevations between the posterior margins of the moderately large elliptical choanae. Males have five to 12 teeth on each process and a total of 10 to 24 (mean, 15.7) prevomerine teeth; females have five to 14 teeth on each process and a total of 10 to 27 (mean, 17.2) prevomerine teeth. The vocal slits are short and extend posterolaterally from the midlateral base of the tongue. The vocal sacs are paired and located behind the angles of the jaws; the sacs are greatly distensible.

The general coloration of *Phrynohyas venulosa* is tan, reddish brown, or pale gray with a large darker mark on the dorsum and transverse bands on the limbs (pl. 46). In specimens from the vicinity of Esparta, Puntarenas Province, Costa Rica, the dorsum varies from yellowish tan with olive-tan markings to reddish brown with dark brown markings. The venter is a dirty white. Individuals from Pal-

mar, Puntarenas Province, Costa Rica, were reddish brown with dark brown dorsal markings and a creamy yellow venter at night. By day they were tan to yellowish tan with dark brown or olive-brown markings. Sixteen individuals from the vicinity of Chepo, Panamá Province, Panamá, all were tan with brown markings and a creamy white venter. One individual from Barranca Bejuco, Michoacán, México, was pale gray with darker greenish gray markings. Three individuals from 3.5 kilometers south of Villahermosa, Tabasco, México, were pale grayish white above and below at night; by day the dorsum changed to uniform gray brown. In all individuals, the iris is a deep golden bronze heavily flecked with black. The deflated vocal sacs are dark brown to black; when the sacs are inflated they are pale brown or olive-brown.

Throughout most of the range of the species in Middle America, the dorsum is marked

by a single large dark blotch. In most specimens from the southern part of the range (Costa Rica and Panamá) the dorsal blotch is distinctly narrower anteriorly than posteriorly (pl. 46, fig. 4). In southern México (Veracruz and Campeche) and Guatemala the dorsal blotch usually is nearly as wide anteriorly as it is posteriorly; however, in many individuals the blotch is interrupted by a medial area of ground color anteriorly (pl. 46, fig. 2). On the Pacific coast of México from Sinaloa to Guerrero many individuals have the dorsal blotch interrupted by a transverse band of ground color in the sacral region (pl. 46, fig. 1). In various parts of the range, unicolor individuals are known; these have been reported from British Honduras, Tabasco, Chiapas, Guatemala, Honduras, El Salvador, and northern Costa Rica. In these individuals, dorsal markings are absent, except that in some of the smaller specimens the warts on the dorsum are tipped with darker pigment (pl. 46, fig. 3). The geographic variation in color pattern in this species has been thoroughly analyzed by McDiarmid (1968).

There is a noticeable ontogenetic change in coloration in this species. Zweifel (1964, p. 205) noted that there is a longitudinal dark stripe on the hind legs of the tadpoles. He stated: "The characteristic pattern of the adult frog is not assumed until several days after metamorphosis appears complete. The dark longitudinal stripe so evident on the hind leg of the large tadpole persists in the newly transformed frog and the variable dark figure on the back is slow to appear, so that for a few days the young frog, with unicolor back and striped legs, looks quite unlike the boldly patterned adult." McDiarmid (1968, p. 16) noted that by the time the frogs reached 24 mm. in snout-vent length, they had attained the adult color pattern.

TADPOLES: Zweifel (1964) described the tadpoles of this species from 5 kilometers south of Bejuco, Panamá Province, Panamá, and Pyburn (1967) described the tadpoles under the name of *Phrynohyas spilomma* from Encinal, Veracruz, México. I have examined the tadpoles from both of these series plus a small series of tadpoles from 34 kilometers north-northwest of Tepic, Nayarit, México.

A typical tadpole in developmental stage 38 from Encinal, Veracruz, México, has a body length of 13.5 mm. and a total length of 41.0 mm. The body is robust and only slightly deeper than wide. In dorsal profile, the snout is bluntly rounded, and in lateral profile, it is round. The eyes are moderately large, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally somewhat below the midline at a point about two-thirds of the distance from the snout to the posterior end of the body. The anal tube is short and median. The caudal musculature is moderately slender and tapers to a fine tip nearly to the terminus of the pointed tail. The ventral fin is somewhat deeper than the dorsal one, which extends onto the body. At midlength of the tail, the depth of the dorsal fin is somewhat greater than the depth of the caudal musculature (fig. 65).

The mouth is medium-sized and antero-ventral in its position. Deep lateral folds are present. The median part of the upper lip is bare; elsewhere, the lips are bordered by two rows of small papillae. Additional rows are present in the lateral folds. The beaks are slender and bear fine serrations. The upper beak is broadly U-shaped with moderately slender lateral processes. The lower beak is broadly V-shaped. In tadpoles of later stages of development, there are four upper and six



FIG. 65. Tadpole of *Phrynohyas venulosa*, K.U. No. 116931. $\times 3$.

lower rows of teeth. The first and second upper rows are present only laterally and in most specimens are fragmented. The third upper row is complete, but the first upper row is narrowly interrupted medially. The first four lower rows are equal in length and somewhat shorter than the third and fourth upper rows. In some specimens, the first lower row is narrowly interrupted medially. The fifth and sixth lower rows usually are fragmented (fig. 66).

In life, specimens from Nayarit were dark olive-brown above; the tail was creamy yellow with a dark brown lateral stripe. The belly was white and the fins were transparent with faint brown flecks. The iris was pale bronze. In preservative, the body is tan with scattered dark brown flecks in larger individuals. The venter is pale creamy tan with scattered brown blotches. The tail is pale cream with a dark brown lateral streak. The fins are transparent with minute flecks. A dark brown stripe is present on the outer edge of the hind limb.

Pyburn (1967, p. 189) commented on the development of the teeth: "In general, the tooth rows nearest the beaks appear before those farthest from the beaks, but there is some variation in the time and sequence in appearance of the rows. Teeth are not apparent in specimens earlier than stage 24. The third and fourth upper and the first and second lower tooth rows are present in stage 25, and the third lower row is usually added later in that stage. The fourth lower row appears in stage 27; the second upper and fifth

lower rows usually develop in stage 28. Specimens in stage 28 have complete beaks, a tooth row formula of 3/5, and little or no indication of tooth resorption. The sixth lower row appears at about stage 31, the first upper row about stage 33, but specimens in stage 33 have 3/5, 3/6, 4/5, or 4/6 rows. After stage 34, the formula is most often 4/6, although the first upper and sixth lower rows may be poorly formed. A few individuals develop a fragmentary lower seventh row, in which case the formula is 4/7."

Zweifel (1964, p. 204) noted that hatching occurs early in stage 18, but Pyburn (1967, p. 190) stated that in Veracruz hatching occurred in stage 17, 24 hours after fertilization. According to Pyburn the length of the tail is less than that of the body in tadpoles in stages earlier than stage 22. From that point in development, the tail becomes progressively longer, until in late stages it is approximately twice the length of the body (table 15).

Pyburn (1967, p. 193) commented that advanced "*P. spilomma*" larvae differ from advanced *P. venulosa* larvae in certain features of the mouthparts and in dorsal pattern. He was particularly concerned that the mouthparts of the tadpoles from Veracruz were not fully developed until about stage 33 or later whereas according to Zweifel's (1964) description of Panamanian tadpoles, the mouthparts obtained full development by stage 27 or 28. Furthermore, Pyburn noted that there were more labial papillae in the specimens from Veracruz than in those from Panamá. It is possible that the degree of development of mouthparts in different stages in the two series could be the result of development at different temperatures, or possibly some other environmental factor. A direct comparison of some of the tadpoles in Pyburn's sample with those described by Zweifel, leave no doubt but that the tadpoles are identical.

MATING CALL: The call of *Phrynohyas venulosa* consists of a loud growl or raucous note regularly repeated at short intervals. An analysis of the recordings of seven individuals from Panamá and Costa Rica show that there is a note repetition rate of 42 to 52 (mean, 47) notes per minute. The duration of each note varies from 0.23 to 0.36 (mean, 0.30) of a second. The notes have 150 to 175 (mean,

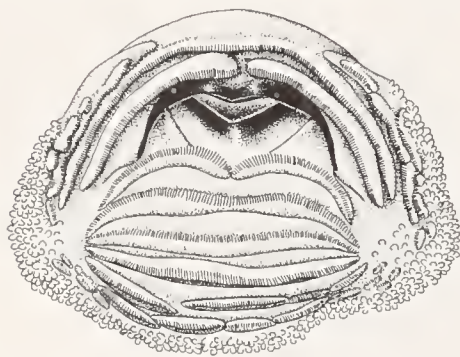


FIG. 66. Mouth of tadpole of *Phrynohyas venulosa*, K.U. No. 116931. $\times 15$.

TABLE 15
Measurements of Tadpoles of *Phrynohyas venulosa*,
with Means in Parentheses, from Encinal, Veracruz, México.^a

Stage	N	Body Length	Tail Length	Total Length
17	5	-----	-----	3.6- 4.1 (3.8)
18	4	-----	-----	3.5- 5.4 (3.9)
19	3	3.8- 3.8 (3.8)	1.7- 1.7 (1.7)	5.5- 5.5 (5.5)
20	15	3.4- 3.8 (3.6)	2.1- 2.7 (2.4)	5.7- 6.1 (6.0)
22	4	3.0- 3.2 (3.0)	3.9- 4.1 (4.0)	6.8- 7.2 (7.0)
23	10	2.9- 3.4 (3.2)	5.2- 6.2 (5.9)	8.1- 9.6 (9.1)
24	6	3.3- 3.7 (3.5)	5.5- 6.8 (6.2)	8.8-10.5 (9.7)
25	2	3.7- 3.8 (3.7)	6.5- 6.5 (6.5)	10.2-10.3 (10.2)
26	10	4.1- 4.7 (4.6)	7.6- 8.4 (7.9)	11.6-13.5 (12.5)
27	10	4.7- 5.6 (5.2)	8.3- 9.5 (8.9)	13.0-15.0 (14.1)
28	10	6.0- 8.8 (7.1)	10.3-15.0 (12.2)	16.3-23.8 (19.3)
31	10	8.5-10.5 (9.5)	16.3-18.4 (17.4)	24.8-28.3 (26.9)
32	4	10.5-11.8 (11.0)	18.8-20.6 (19.5)	29.5-32.4 (30.5)
33	6	10.0-11.9 (10.7)	18.8-23.1 (20.4)	29.3-34.4 (30.5)
34	3	10.4-11.8 (11.3)	19.5-22.5 (21.4)	29.9-34.3 (32.7)
35	5	10.6-13.1 (11.8)	19.5-24.0 (22.2)	30.9-37.1 (34.0)
36	7	11.6-13.0 (12.4)	22.8-25.1 (24.2)	34.8-37.9 (36.6)
37	4	12.0-12.9 (12.6)	25.0-25.9 (25.3)	37.0-38.1 (37.9)
38	4	12.5-13.5 (13.1)	24.9-26.8 (25.8)	37.9-40.1 (38.9)
40	1	13.1	25.8	38.9
41	4	14.0-15.1 (14.5)	27.7-32.6 (29.6)	41.9-47.8 (44.1)
46	1	15.6	-----	-----

^a Data from Pyburn (1967).

161) pulses per second. The notes are well modulated with distinct harmonics; the fundamental frequency varies from 139 to 183 (mean, 159) cycles per second, and the dominant frequency varies from 1392 to 1946 (mean, 1622) cycles per second. In two individuals it is the eighth harmonic that is dominant; in two others the tenth is dominant, and in two others the twelfth is dominant, whereas in another the fourteenth is the dominant harmonic (pl. 36, fig. 3).

Zweifel (1964, p. 202) described the mating call of this species on the basis of a recording of an individual from Neuva Gorgona, Panamá Province, Panamá. The call described by Zweifel is virtually the same as those described here, except that he noted that each note was approximately 0.4 of a second in length and that notes were repeated at about 67 notes per minute. I agree with Zweifel (1964, p. 203) that the description and audiospectrogram of the call of this species given

by Porter (1962, p. 170) is erroneous. Apparently a malfunction in the equipment or an inversion of the audiospectrogram resulted in Porter stating that the dominant frequency of this species is between 6000 and 7000 cycles per second.

NATURAL HISTORY: *Phrynohyas venulosa* is widespread throughout the tropical lowlands of Middle America, where it inhabits areas having a noticeably dry season. It is noticeably absent from the wet Caribbean coastal lowlands from southeastern Nicaragua into Panamá; however, it does occur in the humid Golfo Dulce region. In the dry season, individuals of this species have been found in bromeliads, tree-holes, under the bark of standing trees, and perhaps most frequently beneath the outer sheaths of banana plants. During the dry season, I have observed individuals that are active at night. Apparently the frogs leave their hiding places at dusk to perch on branches or banana plants, where

probably they are engaged in active feeding. On the night of March 29, 1959, at Ciudad Alemán, Veracruz, México, a light rain fell for approximately 15 minutes. Shortly after the rain began one and then somewhat later a second *Phrynohyas venulosa* called intermittently.

Phrynohyas is an opportunistic breeder; apparently heavy rains are necessary to instigate breeding in this species. I have encountered choruses at Amatitlán, Veracruz, México, on July 26, 1956, at Esparta, Costa Rica, on June 21, 1961 (pl. 10, fig. 2), at Palmar, Costa Rica, on April 8, 1966, and near Chepo, Panamá, on June 5, 1966. In each case, the chorus was found immediately after a heavy rain. Zweifel (1964) found calling males near Bejuco, Panamá, on June 4, 1962; Pyburn (1967) encountered choruses at Encinal, Veracruz, México, on June 30, 1964, and June 26, 1966. Porter (1962) reported males calling at Cuautlapam, Veracruz, México, on July 1, 1960, and McDiarmid (1968) obtained calling males from 14.4 kilometers south of Escuinapa, Sinaloa, México, on August 3, 1962. Each of these authors noted that calling males were found only after heavy rains.

Breeding takes place in shallow, temporary ponds. Usually males call while floating on the water or sitting in shallow water; some individuals were observed to cling with their hands to debris floating in the water. Calling sometimes is initiated prior to the arrival of the males at the pond. On June 5, 1966, at a small rainpool 10 kilometers west-southwest of Chepo, Panamá Province, Panamá, I observed several males calling from branches of trees surrounding the pond; later in the evening most individuals were in the water. The calls are produced by inflating the body; then the body is deflated and the air is pushed into the large globular vocal sacs, which resemble balloons on either side of the head. In some individuals, the vocal sacs were observed to touch one another above the head. The call is produced at the time of the inflation of the vocal sacs. At Palmar, Puntarenas Province, Costa Rica, on the night of April 8, 1966, five males were found calling in a shallow temporary pool. In this small chorus there was evidence of social organization in the call structure. One male seemed

to be dominant; it was calling at a distance about 5 meters from the other males. The dominant individual initiated five successive choruses; there was an interval of one to three minutes between choruses. The dominant individual initiated the choruses with a series of notes before the other individuals joined in.

Amplexus is axillary and takes place in shallow water. Pyburn (1967, p. 186) described oviposition at Encinal, Veracruz, México: "The female [of an amplexant pair] suddenly plunged her head below the surface, at the same time extending the hind limbs downward, so that her vent rose about 1 cm. above the water. Her body axis made an angle of approximately 45° with the surface. The male adhered closely to the female's back in axillary amplexus, and eggs were passed while the pair held this tilted position for some five seconds. As the eggs emerged, the female moved her posterior end in rapid side-to-side vibration, possibly to stimulate sperm release by the male. The eggs appeared as an elongate mass, which fell on the water and spread over the surface as a film. After the film had formed, the eggs were about 1 cm. apart in a single layer. The frogs returned to a horizontal position immediately after the egg mass was produced, remained motionless about two minutes, then swam away from the eggs and repeated the performance. I watched another pair deposit eggs in the same manner, captured both pair, and collected an egg sample." Pyburn also noted that when he accidentally struck some freshly laid eggs, the eggs sank, whereas when he struck older eggs with about the same force they remained afloat. Zweifel (1964, p. 203) described the surface film eggs of this species from Panamá and noted that there was a distance of about 1.5 cm. between the eggs and that the single clutch that he observed covered an area of about 1.5 square meters. Zweifel (1968, p. 206) noted that the surface film type of egg mass apparently is an adaptation to relatively low oxygen tension present in warm, standing water characteristic at that breeding site of this species.

Both Zweifel and Pyburn noted the large external gills in early developmental stages. The young tadpoles were observed to hang vertically with their gills spread out over the

surface of the water, an apparent adaptation for survival where dissolved oxygen is in short supply. In Nayarit, México, I obtained advanced larvae stages from a shallow weed-choked pond.

Both Zweifel and Pyburn raised their tadpoles from eggs; the former recorded metamorphosis in 37 days, whereas Pyburn recorded metamorphosis in 47 days. In each case, the metamorphosing young had snout-vent lengths of 15.0 to 16.0 mm. McDiarmid (1968, p. 14) noted recently metamorphosed individuals from Parrita and from Rincón de Osa, Costa Rica, having snout-vent lengths between 13 and 17 mm.

Duellman (1956a, p. 14) described the thick dermal glands on the back of *Phrynohyas* and noted that the center of glandular development is in the occipital region, but that the glands are extensive over the dorsum. He stated that the skin showed a thickened, glandular condition on the head between the orbits, in the occipital region, and in the supratympanic region; the glandular development continues posteriorly on the dorsum for a short distance. Duellman further commented that sections of the skin show that there is a great development of the granular poison glands. They are much larger and more numerous than the mucous glands. The small pustules on the dorsum show the same kind of glandular development but the skin between the pustules and away from the thickened areas has fewer poison glands and proportionately more numerous mucous glands. McDiarmid (1968, p. 20) noted that in specimens collected in late June and July, during the rainy season, the dermal glands in the neck region show relatively little development, whereas the glands in specimens collected in the dry season, in February or March, show extensive development. He noted that in many specimens obtained in the dry season, the glandular development is so extensive that parts of the tympanum are concealed, but that the tympanum is never concealed in Costa Rican specimens taken in the rainy season. McDiarmid (1968, p. 21) stated: "All *Phrynohyas venulosa* examined have these glands, whether the frogs are from areas with a definite wet-dry season or from areas where there is some precipitation throughout

the year. Frogs from the dry forests of Costa Rica, where there is a marked wet-dry season, apparently exhibit a change in the glandular development from season to season. It is suggested that the greater development and subsequent secretion of the glands in the dry season is produced as an adaptive response to arid environments." This suggestion was first made by Neill and Allen (1959, p. 25); these authors, as well as others (Smith, 1941, p. 38; Duellman, 1956a, p. 41) also suggested that the secretions from these dermal glands probably is an effective deterrent to predation. McDiarmid (1968, p. 21) presented a well-documented discussion of slime secretions being a factor in decreasing permeability of the skin to water, a mechanism for the prevention of desiccation that is well documented in lung fish. It is interesting to note that Goeldi (1907, p. 135) and Vellard (1948, p. 150) reported that *Phrynohyas* produced a cutaneous secretion to line the cavities of trees in which they seek refuge. McDiarmid (1968, p. 21) noted that if this is a response to aridity, then this peculiar behavior suggests that *Phrynohyas* has developed a modification to decrease water loss which is similar to that mechanism utilized by the lung fish (Smith, 1961, p. 77-78).

REMARKS: McDiarmid (1968) attempted to explain the geographic variation in size in *Phrynohyas venulosa* in Middle America on the basis of a natural selection for large size in drier environments. In the northern part of the range of the species, the larger individuals are found in dry environments, such as Sinaloa, San Luis Potosí, and Yucatán (compare the sizes of individuals from these areas with those from Veracruz, México, and El Petén, Guatemala, in table 14). The explanation given by McDiarmid is entirely reasonable; however, the largest known specimen of *Phrynohyas venulosa* from anywhere in the range of the species is from Palmar in the wet Golfo Dulce region in southern Costa Rica. This area not only has a high annual rainfall but has rain well distributed throughout the year. An interesting corollary is the gigantic size attained in the Golfo Dulce region as compared with other parts of the range in *Smilisca phaeota*. Perhaps some degree of isolation in population in this area is responsi-

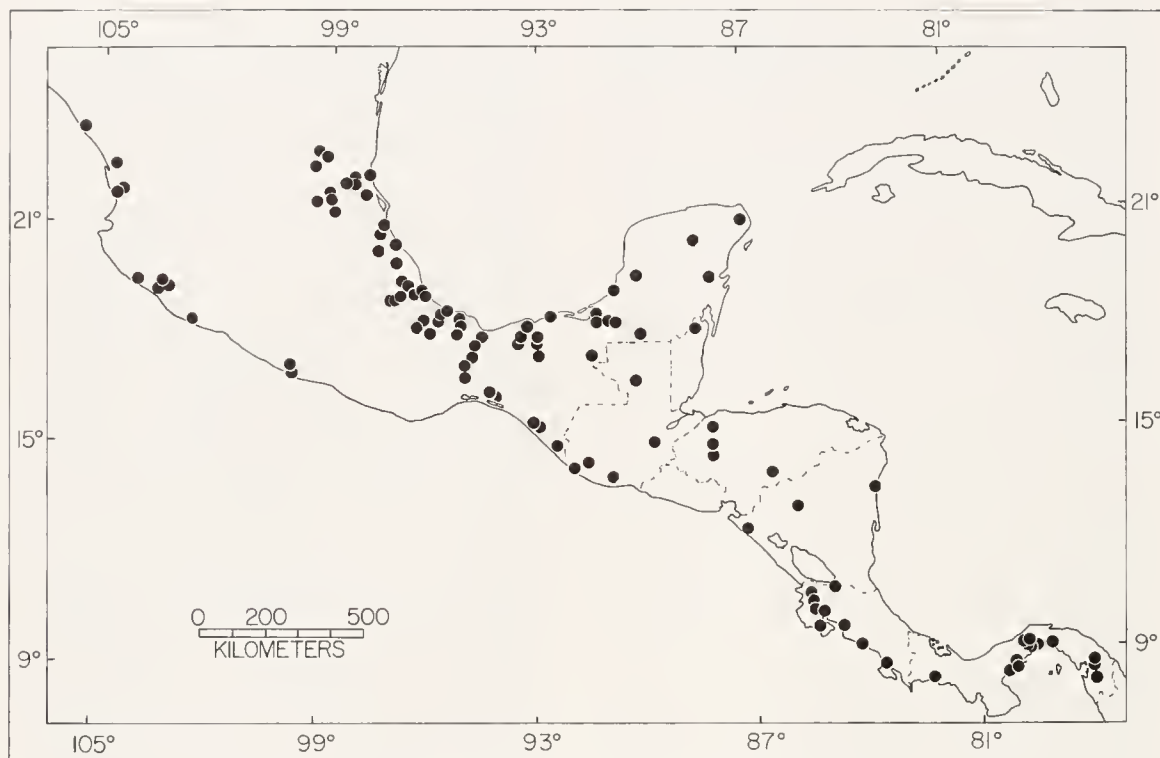


FIG. 67. Distribution of *Phrynohyas venulosa* in Middle America.

ble for differences in size that have resulted through natural selection aside from the general trend towards larger size in drier environments.

Duellman (1956a) recognized four species in Middle America, but later (1966b) showed that one of these (*P. modesta*) was a color variant of *spilomma*. Recently collected material, much of which was analyzed by McDiarmid (1968), confirms the suspicions of the skeptics of Duellman's (1956a) arrangement; all Middle American specimens apparently belong to one highly variable species. The reader is referred to McDiarmid's (1968) detailed discussion of variation.

The venomous properties of the skin secretions of *Phrynohyas venulosa* are well known and have been documented by Duellman (1956a), Shannon and Humphrey (1957), Neill and Allen (1959), and Janzen (1962). The volatile alkaline secretion is insoluble in water and has a deliterious effect on mucous membranes of the eyes and nostrils.

ETYMOLOGY: The specific name is derived from the Latin, *venula*, meaning small veins and the Latin *osus*, meaning full of, and apparently refers either to the secretory properties of the skin or to the areolate or venated pattern on the flanks.

DISTRIBUTION: *Phrynohyas venulosa* is widespread throughout the lowlands of Middle America from central Tamaulipas and southern Sinaloa, México, southward on both coasts to central Nicaragua and thence only on the Pacific lowlands through Panamá (fig. 67). This species generally occurs at elevations below 1000 meters and is absent from the wet forests on the Caribbean lowlands of southern Nicaragua to central Panamá. In South America, this species is widespread in the lowlands east of the Andes.

See Appendix 1 for the locality records of the 786 specimens examined. Neill (1965) and Mertens (1952b) recorded the species from additional localities in British Honduras and El Salvador, respectively.

Genus *Hyla* Laurenti⁶

Hyla Laurenti, 1768, p. 32 [type species, *Hyla viridis* Laurenti, 1768 (= *Rana arborea* Linnaeus, 1758), by subsequent designation (Stejneger, 1907)].

Calamita Schneider, 1799, p. 151 [type species, *Rana arborea* Linnaeus, 1758, by subsequent designation (Stejneger, 1907)].

Hylaria Rafinesque, 1814, fasc. 7 [substitute name for *Hyla*].

Boana Gray, 1825, p. 214 [type species, *Rana boans* Linnaeus, 1758, by monotypy].

Hylaplesia Boie, 1826, p. 239 [type species, *Hyla punctata* Daudin, 1803, by subsequent designation (Stejneger, 1937); preoccupied by *Hylaplesia* Schlegel, 1826 (= *Dendrobates*)].

Hypsiboas Wagler, 1830, p. 200 [type species, *Hyla palmata* Daudin, 1803, by monotypy].

Auletris Wagler, 1830, p. 201 [type species, *Rana boans* Linnaeus, 1758, by subsequent designation (Stejneger, 1907)].

Hyas Wagler, 1830, p. 201 [type species, *Rana arborea* Linnaeus, 1758; preoccupied by *Hyas* Leach, 1815 (Crustacea)].

Scinax Wagler, 1830, p. 201 [type species, *Hyla aurata* Wied, 1825, by subsequent designation (Stejneger, 1907)].

Dendrohyas Wagler, 1830, p. 342 [substitute name for *Hyas* Wagler, 1830; preoccupied by *Hyas* Leach, 1815 (Crustacea)].

Lophopus Tschudi, 1838, p. 32, 73 [type species, *Hyla marmorata* (Laurenti), 1768, by original designation; preoccupied by *Lophopus* Duméril, 1837 (Polyzoa)].

Ranoidea Tschudi, 1838, p. 35 [type species, *Hyla jacksoni* Bilron (in Tschudi, 1838; *nomen nudum*) by monotypy].

Litoria Tschudi, 1838, p. 36 [type species, *Hyla freycineti* Tschudi, 1838, by monotypy].

Hypsipophus Fitzinger, 1843, p. 30 [type species, *Hyla xerophilla* Duméril and Bibron, 1841, by monotypy].

⁶ The most recent synonymy of the genus *Hyla* (Goin, 1961b) differs from that presented here by the omission of two names (*Ololygon* Fitzinger, 1843, and *Pelobius* Fitzinger, 1843), by the exclusion of *Hylonomus* Peters, 1882a (= *Hyloscirtus* Peters, 1882b), and by the inclusion of four names not now considered to be synonyms of *Hyla* (*Phyllodytes* Wagler, 1830); *Palmatorappia* Ahl, 1927; *Pseudohyla* Andersson, 1945; *Limnaeodius* Mittleman and List, 1953). *Phyllodytes* is an older generic name for the frogs formerly placed in the genus *Amphodius* (Bokermann, 1966a). *Palmatorappia* is a ranid. The type species of *Pseudohyla* (*nigrogrisea*) is an *Eleutherodactylus* (fide John D. Lynch, personal communication). The generic status of *Hylodes* *ocularis* Holbrook (type species of the monotypic genus *Limnaeodius*) is open to question; Lynch (1966b) and Chantell (1968) presented osteological data in support of the generic separation from *Hyla*.

Lobipes Fitzinger, 1843, p. 30 [type species, *Hyla palmata* Daudin, 1803, by monotypy; preoccupied by *Lobipes* Cuvier, 1817 (Aves)].

Ostcopilus Fitzinger, 1843, p. 30 [type species, *Trachycephalus marmoratus* Bibron, 1842, in Ramón de la Sagre, by monotypy; *nec* *Hyla marmorata* Laurenti, 1768; (= *Hyla septentrionalis* Duméril and Bibron)].

Phyllobius Fitzinger, 1843, p. 30 [type species, *Hyla albomarginata* Spix, 1824, by monotypy; preoccupied by *Phyllobius* Schönherr, 1824 (Coleoptera)].

Dendropsophus Fitzinger, 1843, p. 31 [type species, *Hyla frontalis* Daudin, 1803, by monotypy].

Dryophytes Fitzinger, 1843, p. 31 [type species, *Hyla versicolor* LeConte, 1825, by monotypy].

Ololygon Fitzinger, 1843, p. 31 [type species, *Hyla strigilata* Spix, 1824, by monotypy].

Pelobius Fitzinger, 1843, p. 31 [type species, *Hyla freycineti* Tschudi, 1838, by original designation].

Centrotelma Burmeister, 1856, p. 97 [type species, *Hyla infulata* Wied, 1825, by monotypy].

Hylomedusa Burmeister, 1856, p. 102 [type species, *Hyla crepitans* Wied, 1824, by monotypy].

Pelodyras Günther, 1859, p. 119 [type species, *Rana caerulea* Shaw, 1802, by monotypy].

Hylella Reinhardt and Lütken, 1862, p. 199 [type species, *Hylella tenera* Reinhardt and Lütken, 1862, by subsequent designation (Smith and Taylor, 1948)].

Cinclidium Cope, 1867a, p. 200 [type species, *Cinclidium granulatum* Cope, 1867a, by monotypy; preoccupied by *Cinclidium* Blyth, 1842 (Aves)].

Chirodryas Kieferstein, 1867, p. 358 [type species, *Chirodryas raniformis* Kieferstein, 1867, by monotypy (= *Hyla aurea* Lesson, 1830)].

Cincloscopus Cope, 1870, p. 554 [substitute name for *Cinclidium* Cope, 1867a; preoccupied by *Cinclidium* Blyth, 1842 (Aves)].

Cophomantis Peters, 1870, p. 650 [type species, *Cophomantis punctillata* Peters, 1870, by monotypy].

Exerodonta Brocchi, 1879, p. 20 [type species, *Exerodonta sumichrasti* Brocchi, 1879, by monotypy].

Hylonomus Peters, 1882a, p. 107 [type species, *Hylonomus bogotensis* Peters, 1882a, by monotypy; preoccupied by *Hylonomus* Dawson, 1860 (Amphibia)].

Hyloscirtus Peters, 1882b, p. 127 [substitute name for *Hylonomus* Peters, 1882a; preoccupied by *Hylonomus* Dawson, 1860 (Amphibia)].

Epedaphus Cope, 1885a, p. 383 [type species, *Hyla gratiosa* LeConte, 1856, by monotypy].

Fanchonia Werner, 1893, p. 82 [type species, *Fanchonia elegans* Werner, 1893 (= *Hyla aurea* Lesson, 1830) by monotypy].

Hyliola Mocquard, 1899b, p. 337 [type species, *Hyla regilla* Baird and Girard, 1852, by subsequent designation (Stejneger, 1907)].

Guntheria Miranda-Ribeiro, 1926, p. 67 [type species, *Hyla dasynota* Günther, 1869 (= *Hyla senicula* Cope, 1868)].

GENEROTYPE: The generic name was proposed by Laurenti (1768, p. 32), who listed nine species in the genus. Stejneger (1907, p. 75) designated *Hyla viridis* Laurenti as the type species of *Hyla*. Most workers, beginning with Daudin (1802, p. 14) have considered *Hyla viridis* Laurenti to be a synonym of *Rana arborea* Linnaeus, 1758. Thus, the generotype of *Hyla* is *Hyla viridis* Laurenti, 1768 (= *Rana arborea* Linnaeus, 1758).

ETYMOLOGY: According to Stejneger (1907, p. 75) the generic name is "Not derived from the Greek word $\nu\lambda\eta$, a wood-land, copse, as commonly stated, but from the vocative of *Hylas*, in Greek mythology, the favorite of Hercules, who lost him in Bithynia, the crying of *hyla*, *hyla* being part of the religious ceremonies instituted in his honor. The croaking of the tree-toad suggested to Laurenti the fanciful idea of its being Hyla's priest, and thus meriting his name, 'haec quasi Hylae sacerdos nomen ejusdem merita est.'"

DEFINITION: The frogs in this genus range in size from minute, delicate frogs, such as *Hyla minuta*, *uana*, and *picta*, having snout-vent lengths of less than 25 mm. to gigantic species, such as *Hyla boans*, *faber*, and *vasta*, some females of which attain snout-vent lengths of 132 mm. The coloration is as variable as size; many small species are nearly uniform yellow, some are green, others are boldly patterned. Bright flash-colors are present in some species; notable among the Middle American species are the red webs in *Hyla loquax* and *rufitela*. The color of the iris is bronze or copper in most species, but it is bright red in members of the *erythromma* and *uranochroa* groups. The palpebral membrane is clear in most species but is reticulated in a few. The pupil is horizontally elliptical. Webbing is absent on the hands in some species, principally the *Hyla eximia* group in Middle America; most species have the fingers one-third to one-half webbed, but in some species in the *boans* and *miliaria* groups, the fingers are fully webbed. The toes are at least half webbed. An axillary membrane, dermal fringes on the limbs, calcar, and thoracic fold are present in some species. The skin is smooth or tuberculate dorsally and always granular ventrally; in some members of the *miliaria* and *septentrionalis* groups the skin

on the top of the head is co-ossified with the underlying cranial bones. In most species the prepollex is enlarged and in breeding males bears a horny nuptial excrescence; in others, the excrescence is absent, whereas in members of the *albomarginata*, *boans*, and *miliaria* groups the prepollex is protruding and in some individuals a projecting prepollical spine is present. A vocal sac is absent in some of the stream-breeding species in the *bistincta*, *mixomaculata*, and *taeniopus* groups, but a single, median, subgular vocal sac is present in most species.

The cranial characters are highly variable; most species have a frontoparietal fontanelle. The quadratojugal is present, reduced, or absent, and the anterior arm of the squamosal does not extend to the maxillary. The medial ramus of the pterygoid is in bony contact with the prootic in some species. Palatines are present in most species (lost in some members of the *rubra* group). Teeth are present on the maxillary and premaxillary, and usually on the prevomer. With the exception of integumentary-cranial co-ossification in two groups and the presence of a dermal sphenethmoid and posterolateral expansions of the frontoparietals in the *septentrionalis* group, striking modifications of dermal cranial elements are lacking.

Insofar as is known, all species have aquatic tadpoles. Some of these develop in ponds, others in streams, and a few in bromeliads or water-filled cavities in trees. The diverse development sites are correlated with a wide variety of morphological types of tadpoles. In some the tail is short with deep fins; in others, the caudal musculature is long and the fins are shallow. The mouth varies in position from anterodorsal, terminal, and anteroventral to ventral. Tadpoles of some species lack teeth, but most have two upper and three lower rows of teeth. The number of tooth rows is higher in many stream-inhabiting tadpoles; proliferation is greatest in the Brazilian *Hyla claresignata*, which has nine upper and 14 lower rows. Among Middle American species, members of the *Hyla mixomaculata* group have the greatest number of tooth rows—seven above and 11 below.

Some stream-breeding species in the *bistincta*, *mixomaculata*, and *taeniopus* groups

lack a voice. Among the vast majority of the Middle American species of *Hyla* the call is well-developed and varies greatly from group to group. Most *Hyla* in the Americas, for which counts are available, have a haploid number of 12 chromosomes; members of the predominantly South American *leucophyllata*, *microcephala*, and *parviceps* groups have 15 chromosomes. The same number of chromosomes is present in the Papuan *Hyla angiana*, whereas other Australo-Papuan species, for which data are available, have a haploid number of 13, the same as the American phyllo-medusine genera (Duellman, 1967b).

COMPOSITION OF GENUS: This immense genus, as now recognized, probably contains more than 300 species. The vast majority of the species occur in South America, and 73 species (five polytypic) are known from Middle America. Four of these are among the 14 occurring in the United States. Of the 73 species from Middle America, I have examined 20,835 preserved frogs, 334 skeletons, 290 lots of tadpoles, and 29 preserved clutches of eggs.

DISTRIBUTION: *Hyla* is nearly world-wide, except for the Antarctic, Arctic, and subarctic regions, Africa south of the Sahara, the islands in the Pacific Ocean, and the southern tip of South America. Species of *Hyla* occur throughout Middle America from sea level to elevations in excess of 3000 meters.

DISCUSSION: I have arranged the 73 Middle American species into 28 species groups, as follows:

1. *rubra* group—24 species, five Middle American (two endemic); a predominately South American group.

2. *microcephala* group—nine species, four Middle American (two endemic); a predominately South American group.

3. *leucophyllata* group—10 species, one Middle American; a predominately South American group.

4. *parviceps* group—eight species, one in lower Central America; a predominately South American group.

5. *albomarginata* group—nine species, one in lower Central America; a predominately South American group.

6. *boans* group—seven species, three in

lower Central America; a predominately South American group.

7. *pseudopuma* group—two species, lower Central American montane pond-breeders.

8. *rivularis* group—four species, lower Central American stream-breeders.

9. *pictipes* group—one species, lower Central American stream-breeder.

10. *uranochroa* group—two species, lower Central American stream-breeders.

11. *lancasteri* group—one species, lower Central American stream-breeder.

12. *zeteki* group—two species, lower Central American bromeliad-breeder.

13. *bogotensis* group—probably at least four species, one in Middle America, lower Central American and northwestern South American stream-breeders.

14. *salvadorensis* group—two species, Central American stream-breeders.

15. *miliaria* group—five species, Mexican and Central American fringe-limbed tree frogs.

16. *godmani* group—two species, Mexican and Central American lowland pond-breeders.

17. *picta* group—two species, Mexican and northern Central American lowland pond-breeders.

18. *miotympanum* group—two species, Mexican stream-breeders.

19. *hazelae* group—two species, Mexican stream-breeders.

20. *erythromma* group—one species, Mexican stream-breeder.

21. *pinorum* group—two species, Mexican stream-breeders.

22. *sumichrasti* group—two species, Mexican stream-breeders.

23. *mixomaculata* group—four species, Mexican stream-breeders.

24. *bromeliacia* group—two species, Mexican and northern Central American bromeliad-breeders.

25. *taeniopus* group—three species, Mexican stream-breeders.

26. *bistincta* group—nine species, Mexican stream-breeders.

27. *eximia* group—seven species, six Mexican; a North American group.

28. *versicolor* group—five species, one Mexican; a North American group.

These groups are treated as units in the

following accounts of the species; the order of presentation does not necessarily follow the proposed phylogenetic relationships. The groups are defined principally on morphological characteristics of the adults and of the tadpoles and secondarily on breeding behavior and distribution. Geographical distribution has influenced the arrangement only in a few cases of morphological similarities in widely disjunct groups of species.

The *Hyla rubra* Group

DEFINITION: The members of this group are small to moderate-sized species. Among the Middle American species, males attain a maximum snout-vent length of 49 mm. and females, 53 mm. (table 16). The dorsum is yellowish tan, gray, or olive-green with darker blotches or longitudinal markings. The posterior surfaces of the thighs are either a uniform yellow or grayish tan, or are marked with broad vertical black bars or black reticulations enclosing yellow spots. The snout is acuminate and protruding, and the palpebral membrane is clear. The webbing is reduced or absent on the hand (fig. 68). The webbing is absent between the first and second toes or reduced to a fringe on the second toe; otherwise the toes are one-half to two-thirds webbed (fig. 69). Dermal folds and appendages are lacking on the limbs, and the axillary membrane is absent. The tarsal fold is weak or absent. Males have a single, median, subgular vocal sac, but lack nuptial excrescences on the pollices. The skull is moderately well ossified (fig. 70) and longer than wide. The large nasals comprise more than 40 per cent of the length of the skull and have long, pointed maxillary processes. The maxillary has a small ventromedial palatine process. The palatines are slender or absent (*H. staufferi*). A frontoparietal fontanelle is present or absent. The sphenethmoid is wider than long. The quadratojugal is slender and always joined to the maxillary by a bony suture. The anterior arm of the squamosal extends about half of the distance to the maxillary. Maxillary, premaxillary, and prevomerine teeth are present. The tadpoles have deep, pointed or xiphicercal tails; the mouth is anteroventral with two upper and three lower rows of teeth and with the median part of

the upper lip devoid of papillae (figs. 71 and 72). The mating call consists of one long, pulsed note or a series of short notes (table 17). In those species for which counts have been obtained the haploid number of chromosomes is 12.

COMPOSITION: About 24 species are currently recognized; most of these occur in southeastern Brasil or in Amazonian South America. Five species, one with two subspecies occur in Middle America. Of these, *Hyla elaeochroa* and *staufferi* are restricted to Middle America. One species, *rostrata*, occurs in Panamá and northern Colombia and Venezuela, whereas *boulengeri* occurs on the Pacific lowlands of South America, and *rubra* is widespread in South America. Of the five Middle American species, 3113 preserved frogs, 52 skeletons, 12 lots of tadpoles, and three preserved clutches of eggs have been examined.

COMMENTS: The taxonomy of the *Hyla rubra* group was treated in detail by León (1969); much of the information presented in the following accounts of the species is summarized from his work.

The *Hyla rubra* group is highly diversified in South America. The taxonomy of the group is complex and poorly understood. Apparently at least two subgroups are present in South America. One of these contains the medium-sized species and is represented in Middle America by *boulengeri* and *rostrata*. The second group is composed of smaller frogs and is represented in Middle America by *elaeochroa*, *rubra*, and *staufferi*. Evidently the differentiation of these groups took place in South America prior to the late Pliocene.

The osteological characters given in the preceding definition are constant among those species of the group that have been studied. Other aspects of the cranial osteology show specific differences (fig. 70); some of these are compared in table 18, and all of them are described by León (1969).

The tadpoles of *Hyla rubra* and *elaeochroa* are alike in having xiphicercal tails and moderately low fins. The tadpoles of *staufferi* are somewhat intermediate in shape and proportions between the former and the tadpoles of *boulengeri* and *rostrata*, which have deep caudal fins (figs. 71 and 72). Tadpoles of *bou-*

TABLE 16

Comparison of Measurements and Certain Proportions, with Means in Parentheses, of Middle American Species in the *Hyla rubra* Group.^a

Species	Sex	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
<i>H. rubra</i> ^b	♂	45	27.1-35.2 (31.8)	0.492-0.558 (0.518)	0.392-0.458 (0.437)	0.339-0.409 (0.366)	0.300-0.342 (0.321)	0.473-0.702 (0.564)
	♀	20	34.1-40.8 (37.8)	0.486-0.549 (0.523)	0.386-0.458 (0.435)	0.330-0.400 (0.362)	0.278-0.341 (0.320)	0.564-0.718 (0.633)
<i>H. elaeochroa</i>	♂	259	26.3-37.7 (31.5)	0.471-0.566 (0.515)	0.361-0.498 (0.417)	0.314-0.379 (0.345)	0.284-0.347 (0.312)	0.444-0.683 (0.557)
	♀	36	30.4-40.3 (35.0)	0.483-0.561 (0.528)	0.391-0.466 (0.430)	0.322-0.367 (0.347)	0.298-0.341 (0.316)	0.493-0.687 (0.596)
<i>H. s. stauferi</i>	♂	471	20.6-29.0 (25.4)	0.414-0.538 (0.475)	0.314-0.446 (0.394)	0.298-0.378 (0.332)	0.233-0.346 (0.288)	0.463-0.768 (0.600)
	♀	61	21.3-31.6 (27.1)	0.433-0.528 (0.488)	0.342-0.448 (0.393)	0.303-0.378 (0.339)	0.264-0.318 (0.294)	0.464-0.746 (0.620)
<i>H. stauferi altae</i>	♂	56	21.7-26.0 (23.7)	0.413-0.498 (0.463)	0.342-0.413 (0.388)	0.311-0.349 (0.340)	0.244-0.302 (0.287)	0.452-0.719 (0.572)
	♀	3	26.8-27.8 (27.1)	0.455-0.477 (0.463)	0.384-0.390 (0.387)	0.332-0.347 (0.340)	0.280-0.291 (0.287)	0.541-0.583 (0.563)
<i>H. Boulengeri</i>	♂	106	35.6-48.7 (41.6)	0.512-0.610 (0.554)	0.353-0.462 (0.427)	0.351-0.412 (0.379)	0.312-0.359 (0.339)	0.533-0.798 (0.708)
	♀	13	41.6-52.8 (48.0)	0.537-0.610 (0.581)	0.413-0.468 (0.439)	0.369-0.396 (0.373)	0.329-0.362 (0.334)	0.657-0.829 (0.746)
<i>H. rostrata</i>	♂	28	40.0-45.7 (42.5)	0.541-0.609 (0.572)	0.403-0.461 (0.432)	0.352-0.397 (0.371)	0.302-0.354 (0.323)	0.563-0.811 (0.672)
	♀	1	41.0	0.585	0.460	0.350	0.336	0.763

^a Based in part on data presented by Léon (1969).

^b Sample composed of 10 specimens from eastern Panamá and 55 from Napo Province, Ecuador.



FIG. 68. Hands of the Middle American species in the *Hyla rubra* group. A. *H. rubra*, K.U. No. 109471. B. *H. elaeochroa*, K.U. No. 64426. C. *H. s. staufferi*, K.U. No. 57826. D. *H. boulengeri*, K.U. No. 101544. E. *H. rostrata*, K.U. No. 77164, $\times 7$.



FIG. 69. Feet of the Middle American species in the *Hyla rubra* group. A. *H. rubra*, K.U. No. 109471. B. *H. elaeochroa*, K.U. No. 64426. C. *H. s. staufferi*, K.U. No. 57826. D. *H. boulengeri*, K.U. No. 101544. E. *H. rostrata*, K.U. No. 77164. $\times 5$.

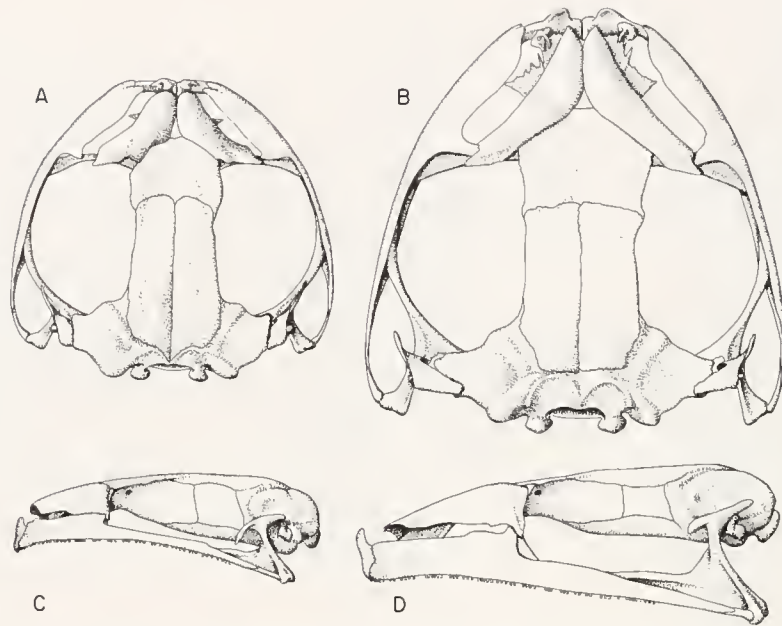


FIG. 70. Dorsal and lateral views of skulls of members of the *Hyla rubra* group. A and C. *H. elaeochroa*, K.U. No. 104356. B and D. *H. rostrata*, K.U. No. 104349. $\times 5$.

lengeri are unique in the group by lacking papillae on the lower lip and by having greatly elongated teeth in the third lower tooth row.

The mating calls of *Hyla rubra*, *elaeochroa*, and *staufferi* consist of series of short notes, whereas the calls of *boulengeri* and *rostrata* consist of one moderately long note. The calls of all of the species, except that of *rubra*, are characterized by two emphasized harmonics (one between 900 and 2100 cycles per second and another between 1900 and 4100 cycles per second). In *rubra* only the lower frequency is emphasized. The calls of the various species also exhibit differences in pulse rate and fundamental frequency (table 17).

The *Hyla rubra* group is a post-Pliocene invader in Middle America. León (1969) has postulated the differentiation of *elaeochroa* from *rubra* in Central America through spatial isolation—*elaeochroa* in humid Caribbean environments in Central America and *rubra* in South America. In Central America the latter species occurs now only in eastern Panamá. León suggested that the *elaeochroa* stock differentiated into *elaeochroa* on the

humid Caribbean lowlands and into *staufferi* on the xeric Pacific lowlands. The differentiation of *staufferi* probably was in response to the drier environment. The xeric adapted *staufferi* was able to disperse through sub-humid environments northward into México. The humid Golfo Dulce region in southeastern Costa Rica is a hiatus in the present distribution of *Hyla staufferi*; the subspecies *staufferi* occurs to the north and west of Golfo Dulce, and *altae* inhabits the dry country to the east of Golfo Dulce. León further hypothesized that *boulengeri* invaded Central America from South America in the late Pliocene and inhabited the humid Caribbean lowlands. León suggested that a peripheral population was isolated on the xeric Pacific lowlands of Panamá where it differentiated into *rostrata*, which subsequently expanded its range into South America. Perhaps it is equally plausible that *rostrata* differentiated from *boulengeri* in South America and that they each entered Central America as distinct species, *rostrata* following the xeric dispersal route and *boulengeri* following the humid dispersal route.

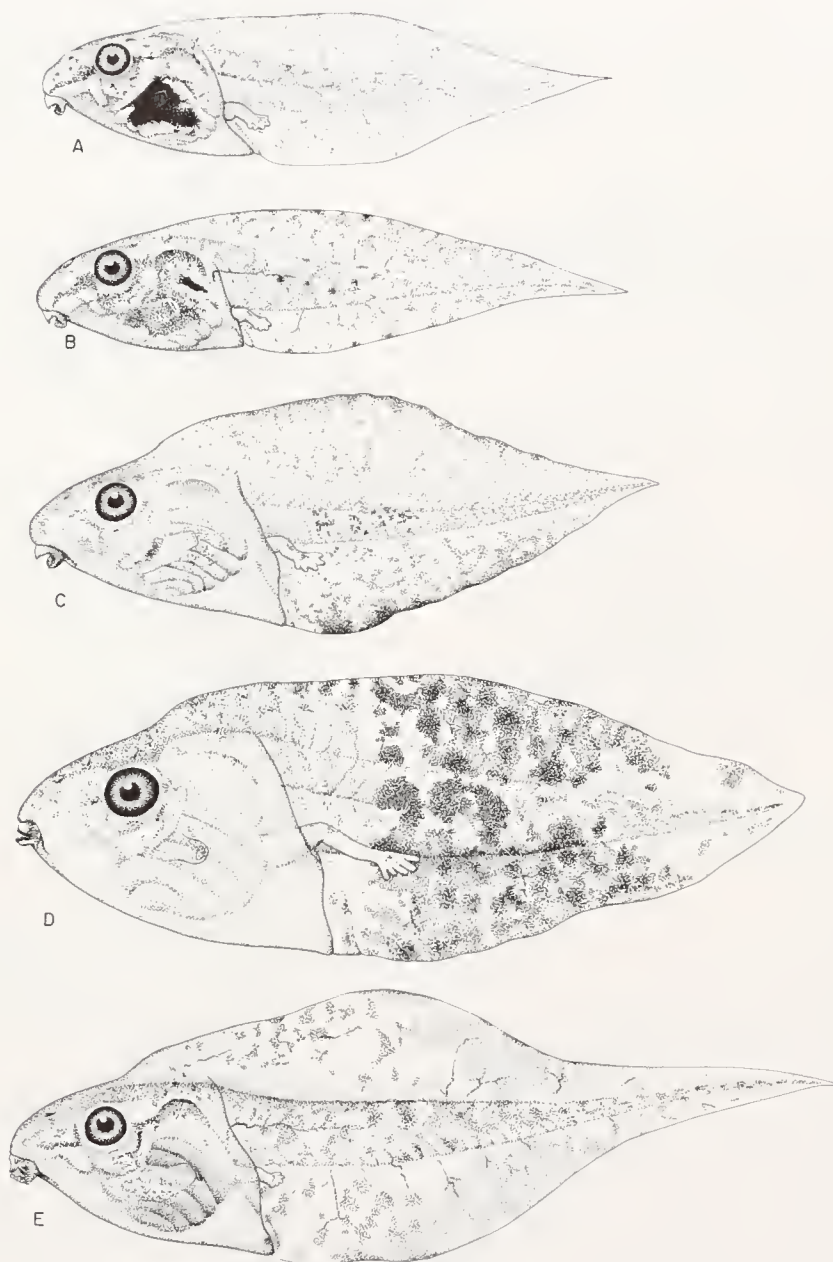


FIG. 71. Tadpoles of the Middle American species in the *Hyla rubra* group. A. *H. rubra*, K.U. No. 109492. B. *H. elaeochroa*, K.U. No. 104134. C. *H. staufferi*, K.U. No. 104162. D. *H. Boulengeri*, K.U. No. 104295. E. *H. rostrata*, K.U. No. 104244. $\times 3$.

TABLE 17

Comparison of the Mating Calls, with Means in Parentheses, of the Middle American species in the *Hyla rubra* Group.^a

Species	N	Notes per call group	Duration of note (sec.)	Pulse Rate (sec.)	Fundamental Frequency (cps)	Major Frequencies (cps) Lower	Upper
<i>H. rubra</i> ^b	5	1-10 (3)	0.12-0.15 (0.13)	61-65 (63)	58-64 (61)	1545-1636 (1581)	-----
<i>H. elaeochroa</i>	15	2-95 (19)	0.12-0.24 (0.17)	40-50 (42)	48-65 (57)	1254-1586 (1499)	2562-3477 (2911)
<i>H. s. staufferi</i>	18	2-77 (23)	0.12-0.23 (0.18)	100-130 (120)	96-130 (106)	1582-1872 (1743)	1962-3744 (3056)
<i>H. s. altae</i>	7	2-22 (11)	0.14-0.18 (0.15)	110-130 (120)	104-117 (112)	1853-2106 (2008)	3379-4056 (3775)
<i>H. boulengeri</i>	8	1	0.24-0.47 (0.35)	80-120 (101)	70-74 (71)	1400-1820 (1611)	2520-3182 (2840)
<i>H. rostrata</i>	7	1	0.23-1.86 (0.69)	50-60 (51)	52-61 (56)	912-1026 (918)	2736-3477 (3055)

^a Data, except for *Hyla rubra*, from Léon (1969).

^b Calls recorded at Santa Cecilia, Napo Province, Ecuador.

TABLE 18

Comparison of Cranial Characters in the Middle American Species in the *Hyla rubra* Group.

Character	<i>H. rubra</i> ^a	<i>H. elaeochroa</i>	<i>H. staufferi</i>	<i>H. boulengeri</i>	<i>H. rostrata</i>
Maxillary	Depth of pars facialis 2X	Depth of pars facialis 2X	Depth of pars facialis 2X	Depth of pars facialis 4X	Depth of pars facialis <3X
Nasal	pars dentalis Truncate anteriorly	pars dentalis Truncate anteriorly	pars dentalis Round anteriorly	pars dentalis Pointed anteriorly	pars dentalis Pointed anteriorly
Frontoparietal fontanelle	Anteriorly Absent	Anteriorly Present	Anteriorly Present	Anteriorly Present	Anteriorly Absent
Squamosal	Posterior	Posterior	Posterior	Posterior	Posterior
Palatine	arm round terminally Present	arm round terminally Present	arm pointed terminally Absent	arm pointed terminally Present	arm round terminally Present

^a Based on specimens from Napo Province, Ecuador; the characters do not necessarily hold for all specimens currently assigned to *Hyla rubra*. For example, specimens from Jacareacanga, Estado Pará, Brasil, have a frontoparietal fontanelle.

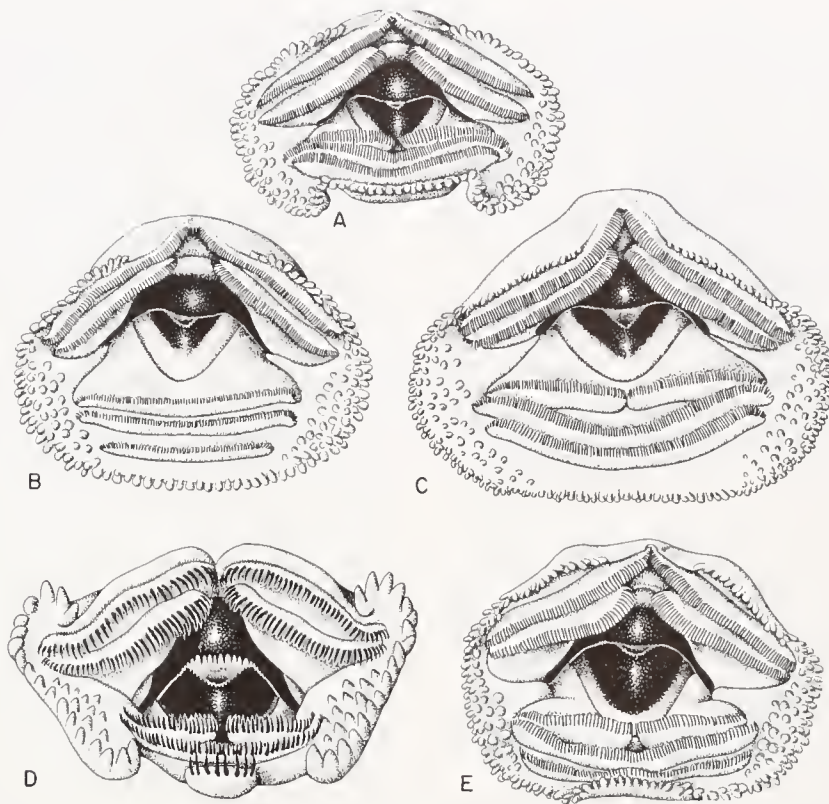


FIG. 72. Mouthparts of tadpoles of the Middle American species in the *Hyla rubra* group. A. *H. rubra*, K.U. No. 109492. B. *H. elaeochroa*, K.U. No. 104134. C. *H. staufferi*, K.U. No. 104162. D. *H. Boulengeri*, K.U. No. 104295. E. *H. rostrata*, K.U. No. 104244. $\times 20$.

An adequate understanding of the *Hyla rubra* group must await a thorough study of the many species in South America.

Hyla rubra Laurenti

Hyla rubra Laurenti, 1768, p. 35 [no specimen designated; locality "America"]. Daudin, 1802, p. 26 [no specimen designated; locality, "Surinam"; Marin de Baize collector (?)]. Boulenger, 1882a, p. 403. León, 1969, p. 524.

Calamita rubra: Merrem, 1830, p. 171.

Auletris rubra: Wagler, 1830, p. 201.

Dendrohyas rubra: Tschudi, p. 74.

Scytotis ruber: Cope, 1874, p. 124.

Hyla elaeochroa (part): Dunn and Emlen, 1932, p. 25.

DIAGNOSIS: *Hyla rubra* can be distinguished from other Middle American species in the *Hyla rubra* group by having bold dark brown or black reticulations enclosing bright yellow (creamy tan in preservative) spots on

the posterior surfaces of the thighs. Structurally, *rubra* is similar to *elaeochroa*, which differs in having the posterior surfaces of the thighs uniform pale yellow or with suffuse olive-tan mottling. Furthermore, in most specimens of *rubra* distinct pale dorsolateral stripes, and usually a middorsal stripe, are present. In *elaeochroa* the stripes, if present, are only faintly discernible in most specimens. Other Middle American species in the *Hyla rubra* group differ from *rubra* either by being smaller and having uniformly colored thighs (*staufferi*) or by being larger and having vertical black bars on the posterior surfaces of the thighs (*Boulengeri* and *rostrata*). The protruding snout, reduced web between the first and second toes, and reticulate pattern on the posterior surfaces of the thighs distinguish *rubra* from all other Middle American hylids.

DESCRIPTION: This is a medium-sized species in the *Hyla rubra* group. Adult males attain a snout-vent length of 35.2 mm., and females reach 40.8 mm. In a series of 17 males from Santa Cecilia, Napo Province, Ecuador, the snout-vent length is 30.9 to 33.6 (mean, 32.2) mm.; the ratio of the tibia length to snout-vent length is 0.496 to 0.520 (mean, 0.510); the ratio of foot length to snout-vent length is 0.420 to 0.453 (mean, 0.443); the ratio of head length to snout-vent length is 0.354 to 0.377 (mean, 0.367); the ratio of head width to snout-vent length is 0.310 to 0.324 (mean, 0.317), and the ratio of the diameter of the tympanum to that of the eye is 0.486 to 0.563 (mean, 0.537). In four females from the same locality the snout-vent length is 37.2 to 40.1 (mean, 38.6) mm. The females differ from the males in having a proportionately larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.577 to 0.609 (mean, 0.592). No significant differences in size or proportions exist between the samples from Napo Province, Ecuador, and the few specimens available from eastern Panamá.

The head is slightly narrower than the body, and the top of the head is barely convex. In dorsal profile the snout is acutely rounded with a small terminal point; in lateral profile the snout is acutely rounded and noticeably protruding beyond the leading edge of the lower jaw. The snout is long; the nostrils are noticeably protuberant and situated about three-fourths the distance from the eyes to the tip of the snout. The canthus is round and indistinct. The loreal region is barely concave and is inclined laterally; the lips are thin and flared. An indistinct dermal fold extends from the posterior edge of the eye, above the tympanum, and downward to a point above the insertion of the arm. In some specimens this fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately long and slender; an abbreviated axillary membrane is present. There are no tubercles or dermal folds along the ventrolateral edge of the forearm, but a distinct dermal fold is present on the wrist. The fingers are moderately long and

slender and have large, bluntly rounded (nearly truncate) discs. The width of the disc on the third finger is slightly greater than the diameter of the tympanum. The subarticular tubercles are small and conical; none is bifid, and the distal tubercles on the first and fourth fingers are noticeably larger than the others. The supernumerary tubercles are small and subconical; they are arranged irregularly or in two rows on the proximal segments of the digits. A broad, flat, bifid or tripartite outer palmar tubercle is present. The prepollex is barely enlarged, and in breeding males there is no nuptial excrescence. Webbing is absent between the fingers (fig. 68A). The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A distinct transverse dermal fold is present on the heel, but the tarsal fold is absent. The inner metatarsal tubercle is broad, low, flat, and not visible from above. The outer metatarsal tubercle is distinct and conical. The toes are moderately long and slender; they bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are low and subconical. Distinct, conical supernumerary tubercles are present in a single row on the proximal segment of each digit. The toes are about three-fourths webbed (fig. 69A). Between the first and second toes the webbing is present only as a fringe along the edge of the second toe; the webbing extends from the distal end of the penultimate phalanx of the second to the distal end of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed ventrally near the upper levels of the thighs and is covered by a short, down-curved anal sheath. Anal tubercles are absent. The skin is granular on the belly and on the proximal posteroventral surfaces of the thighs; elsewhere the skin is smooth. The tongue is cordiform, shallowly notched behind, and barely free posteriorly. The dentigerous processes of the prevomers are elevated posterolaterally inclined ridges between the small ovoid choanac. Males have

four to six teeth on each ridge and a total of nine to 12 teeth (mean, 17 specimens from Santa Cecilia, 10.6). Females have six to eight teeth on each ridge and a total of 13 to 16 teeth (mean, four specimens from Santa Cecilia, 14.2). The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subangular, and moderately distensible.

Because the color pattern is faded in most of the existing museum specimens of *Hyla rubra* from Central America and because I have not seen living specimens of this species from Central America, unless otherwise indicated, the following notes on coloration are based on specimens from Napo Province, Ecuador. The general coloration of *Hyla rubra* is pale olive-brown or grayish brown with lighter longitudinal markings (pl. 47, fig. 4). At night the frogs are pale dull yellow with or without faint tan dorsal markings. The posterior surfaces of the thighs, and in some specimens, the anterior surfaces of the thighs also, are yellow with dark brown or black mottling. The belly is creamy yellow and the vocal sac is bright yellow. By day, the dorsum is tan, brown, or gray with pale longitudinal markings. The mottling on the flanks and thighs is more contrasting than at night. In some specimens, the flanks are yellow with brown or black reticulations tending to enclose small yellow spots. In other individuals the flanks are creamy yellow with black, brown, or olive flecks. In all individuals, the proximal anterior surfaces of the thighs, posterior surfaces of the thighs, and the inner surfaces of the shanks have dark brown or black reticulations enclosing deep yellow spots (fig. 73). In some specimens, the groin is immaculate yellow. The iris is bronze with black reticulations.

In preservative, the dorsum is tan or olive-brown, usually with distinct dorsolateral creamy tan or dull grayish tan stripes that extend to the sacral region. In some individuals a distinct, irregular middorsal stripe is present. The flanks are creamy tan with brown flecks or mottling. The proximal anterior surfaces of the thighs, the posterior surfaces of the thighs, and the inner surfaces of the shanks are creamy tan with dark brown or black reticulations or mottling. The venter is creamy white. Faint transverse bands are



FIG. 73. Posterior surface of right thigh of *Hyla rubra* showing typical color pattern, K.U. No. 109470. $\times 4$.

discernible on the dorsal surfaces of the shanks and feet in some individuals.

The coloration of the posterior surfaces of the thighs of the Panamanian specimens is variable. In most individuals, the reticulations are less well developed than in the Ecuadorian specimens. In some specimens, such as M.C.Z. No. 13248 and U.S.N.M. No. 37863, an elongate creamy yellow bar on the posterior surfaces of the thighs is narrowly outlined with black. In one specimen from Madden Dam (F.M.N.H. No. 67820) dark spots are present in the groin, on the ventral surfaces of shanks, and on the anterior surfaces of the thighs, but the posterior surfaces of the thighs are marked only by a small longitudinal yellow mark proximally that is outlined by black. In M.C.Z. No. 1398, the posterior surfaces of the thighs are marked by narrow, short vertical black lines, and in M.C.Z. No. 17581 three or four small black spots are present on the posterior surface of each thigh. In M.C.Z. No. 1399 the dorsum is cream with dark brown and black mottling extending on to the dorsal surfaces of the limbs, the posterior surfaces of the thighs, and into the groin; the anterior surfaces of the thighs and ventral surfaces of the shanks and thighs are creamy tan with small brown spots. Two specimens from El Real, Darién Province, Panamá (U.S.N.M. Nos. 140571 and 140572), lack spots or markings in the groin and on the thighs and shanks. Otherwise, they do not differ from the specimens of *Hyla rubra*.

TADPOLES: No tadpoles of this species are

known from Central America. The following description is based on specimens obtained at Santa Cecilia, Napo Province, Ecuador (K.U. No. 109492). A typical tadpole in developmental stage 36 has a body length of 8.4 mm. and a total length of 24.3 mm. The body is slightly deeper than wide. In dorsal profile the snout is bluntly rounded and in lateral profile more acutely rounded. The nostrils are large, situated midway between the eyes and the tip of the snout and directed anterodorsally. The eyes are moderately large and directed laterally. The spiracle is sinistral, and the spiracular opening is below the midline at a point about two-thirds the length of the body. The anal tube is moderately long and sinistral. The caudal musculature is slender and tapers to a very slender tip distally. At midlength of the tail the musculature is shallower than either the dorsal or ventral fin. The dorsal fin extends well onto the body; terminally, the fins are shallow, so as to form a xiphicercal tail (fig. 71A).

In life, the body is iridescent silvery-gold laterally. The dorsum and the dorsal fin are yellowish tan with darker brown flecks. In preservative the body is creamy tan. A brown stripe extends from the snout to the eye. Brown spots are present on the sides of the body and on the caudal musculature, and gray flecks are present on the fins.

The mouth is small and anteroventral in position. Deep lateral folds are present in the lips. The median part of the upper lip is bare; the rest of the upper lip is bordered by one row of long papillae. Two or three rows of papillae are present on the lower lip, and additional papillae are present in the lateral fold. The beaks are robust and bear fine serrations. The upper beak is in the form of a broad arch with slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length and extend to the labial papillae; the second upper row is narrowly interrupted medially. The lower rows are slightly shorter than the upper ones; the third lower row is shorter than the others. All lower rows are complete (fig. 72A).

MATING CALL: Calls of *Hyla rubra* were recorded at Santa Cecilia, Napo Province, Ecuador. The calls have one to 10 notes per

call group; call groups are repeated at intervals of four to 33 seconds. The short notes have a duration of 0.12 to 0.15 of a second and a pulse rate of 61 to 65 pulses per second. The average fundamental frequency is 61 cycles per second and the average dominant frequency is 1581 cycles per second (table 17, pl. 27, fig. 1).

NATURAL HISTORY: No definite information is available concerning the natural history of *Hyla rubra* in Central America. On the basis of the localities from which the species is known in Central America, it can be surmised that it is a species that breeds in the rainy season in shallow, temporary ponds. In Napo Province, Ecuador, *Hyla rubra* is one of the most abundant hylids in the tropical rain forest. By day, individuals were found in bromeliads and in other sheltered places above the ground. Males call from bushes and herbs at the edge of small rain pools. Gravid females were abundant in February, March, and June.

The tadpoles develop in shallow muddy pools, where they hide amidst the aquatic vegetation and frequently swim to the surface. When disturbed, the tadpoles seek refuge in the vegetation or in the mud at the bottom of the pool.

REMARKS: The use and application of the name of *Hyla rubra* is confused. León (1969, p. 524) discussed the nomenclatural problems regarding *Hyla rubra*: "The taxonomic history of *Hyla rubra* Laurenti is confused. Seba (1734:70) illustrated and diagnosed a form for which he used the name 'Ranula, Americana, Rubra.' Linnaeus (1758:213) considered Seba's frog to be a variety of *Hyla arborea*. Laurenti (1768:35) apparently examined the same individual that Seba called 'Ranula, Americana, Rubra.' For this specimen, Laurenti used the binomial *Hyla rubra* and provided a brief diagnosis. The type locality was given as 'America.'

"Daudin (1802:26) redescribed the same specimen(s?) treated by Seba and Laurenti and provided a fairly good description and figure. Daudin restricted the type locality to Surinam and indicated that Marin de Baize was the probable collector. Daudin (1802:26 and 1803:53) neglected to consider Laurenti's work, but he applied the same name used by

Laurenti. Most authors have credited *Hyla rubra* to Daudin, but Rivero (1961:120) noted that *Hyla rubra* Laurenti, 1768, has priority over *Hyla rubra* Daudin, 1802. Since both Laurenti and Daudin worked on Seba's material, it is reasonable to assume that Daudin redescribed the same frogs that were named by Laurenti; this was not an uncommon practice in the early nineteenth century. Thus, I conclude that *Hyla rubra* Daudin, 1802, is a junior primary homonym of *Hyla rubra* Laurenti, 1768."

The matter of the authority for the name is problematical. It is impossible to determine whether Daudin merely redescribed the frog named *Hyla rubra* by Laurenti or whether he inadvertently proposed the same specific name for what might be a different species of frog. Because there is no way of definitely settling this question, I agree with León that it is best to consider *Hyla rubra* Daudin, 1802, to be a junior primary homonym of *Hyla rubra* Laurenti, 1768. Even if the nomenclature is settled in this manner, the biological problem of the application of the name *Hyla rubra* to a definite population of frogs still remains. At this time, the taxonomy of *Hyla rubra* in South America is too poorly known to determine whether or not the widespread species now known as *Hyla rubra* is actually one species or a composite of two or more species. Consequently, I have chosen the conservative approach and have applied the name *Hyla rubra* to the Central American populations.

Dunn (1931b, p. 413) reported *Hyla rubra* from the Canal Zone and San Pablo, Panamá. Subsequently, Dunn and Emlen (1932, p. 25) and Dunn (1933, p. 61) listed specimens of *Hyla rubra* from Nicaragua, Costa Rica, and western Panamá. At that time, Dunn was under the impression that *Hyla elaeochroa* was a synonym of *Hyla rubra*. Subsequent study has revealed that *Hyla elaeochroa* is a distinct species. Consequently, the records of *Hyla rubra* reported by Dunn and Emlen, and by Dunn in his later paper are actually based on *Hyla elaeochroa*.

Three specimens from El Real, Darién Province, Panamá (U.S.N.M. Nos. 140569, 140570, and 140573), are discussed here, although these individuals probably do not represent *Hyla rubra*. All three are males, having

snout-vent lengths of 40.6 to 42.6 (mean, 41.1) mm. Thus, they are larger than the known females from Panamá, in which the snout-vent length is 35.5 to 40.8 (mean, 4 specimens, 38.4) mm. In proportions, these three males differ from six males of *Hyla rubra* from Panamá by having proportionately shorter tibia and narrower heads. In these three males, the ratio of the tibia length to the snout-vent length is 0.484 to 0.512 (mean, 0.496), as compared with 0.501 to 0.548 (mean, 0.528) in Panamanian *Hyla rubra*. The ratio of head width to snout-vent length is 0.295 to 0.315 (mean, 0.306), as compared with 0.300 to 0.342 (mean, 0.331). Likewise, the tympanum is proportionately larger in these three males; the ratio of the diameter of the tympanum to that of the eye is 0.600 to 0.619 (mean, 0.611), as compared with 0.473 to 0.667 (mean, 0.559) in the Panamanian *Hyla rubra*. The three males from El Real have no spots or markings in the groin. The flanks are plain or weakly mottled; small black spots are present on the anterior surfaces of the thighs and on the ventral surfaces of the shanks. The posterior surfaces of the thighs are pale brown with an elongate creamy white spot in which black dashes or small spots are present. I have no knowledge of the coloration of these frogs in life. It is highly probable that these three specimens represent a species distinct from *Hyla rubra*. Similar large *rubra*-like frogs are known to occur sympatrically with *Hyla rubra* in northern Venezuela and the Guianas, but the taxonomic status of these, like those in Panamá, is unknown.⁷

ETYMOLOGY: The specific name *rubra* is Latin meaning red. The application of this specific name by Laurenti and Daudin apparently is based on Seba's usage of the name.

DISTRIBUTION: In Central America, *Hyla rubra* is known from the Canal Zone and eastward on the Pacific lowlands of Panamá (fig.

⁷ Recently I have seen additional specimens of this large *H. rubra*-like frog from Achioté, Colón Province, Panamá (U.F. Nos. 27001-12, 27018) and from Yavisa, Darién Province, Panamá (M.V.Z. Nos. 83191-98). A recent specimen (K.U. No. 125026) from 5 kilometers east of Achioté, Colón Province, Panamá, collected by Dr. Sam R. Telford, Jr., is a member of the *Hyla rubra* group but is unlike any other specimen of the group known to me. Possibly the specimen is a hybrid between *rubra* and *boulengeri*.

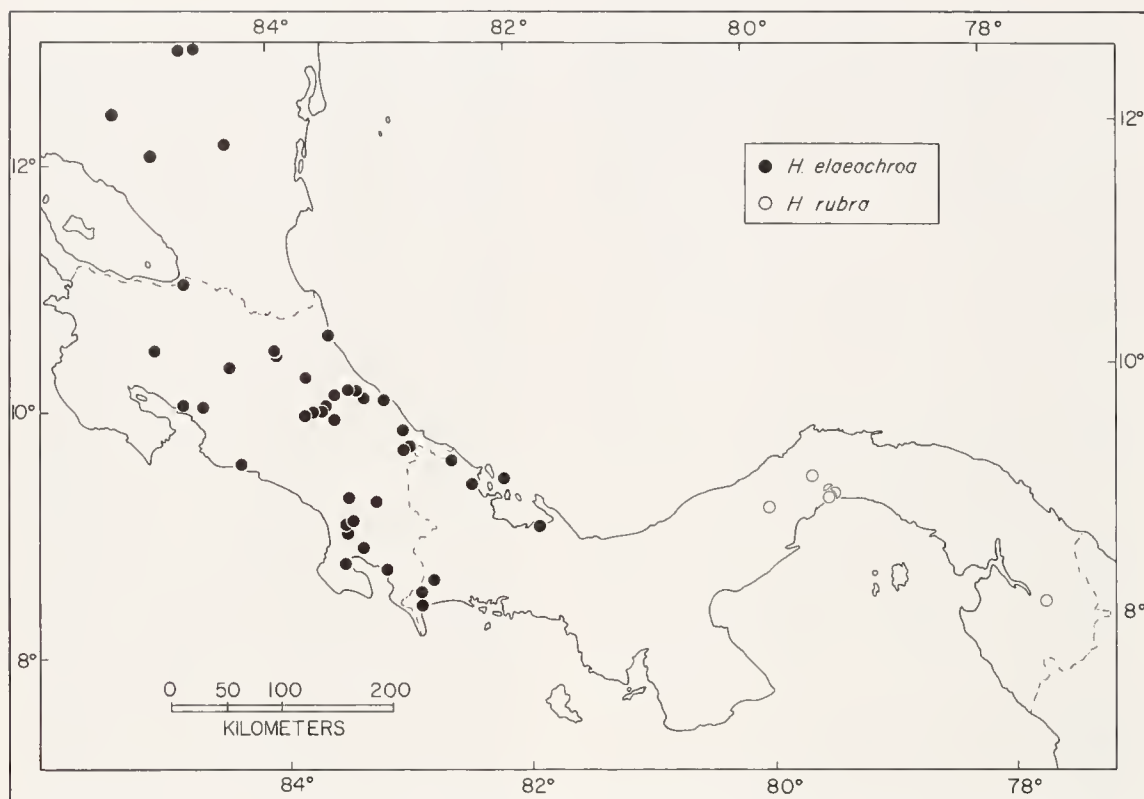


FIG. 74. Distribution of *Hyla rubra* and *Hyla elaeochroa*.

74). In South America, the frogs known by the name of *Hyla rubra* occur throughout the lowlands of northern South America and of the Amazon Basin.

See Appendix I for the locality records of the 32 specimens examined.

Hyla elaeochroa Cope

Hyla elaeochroa Cope, 1876 [lectotype, U.S.N.M. No. 30689 from the east foot of mountains near Sipurio, Limón Province, Costa Rica; William M. Gabb collector]. Brocchi, 1882, p. 39. Boulenger, 1882a, p. 399. Günther, 1901 (1885-1902), p. 265. Taylor, 1952c, p. 859. Duellman, 1966b, p. 270. León, 1969, p. 525.

Hyla quinquevittata Cope, 1886 [holotype, U.S.N.M. No. 14187 from "Nicaragua"; John F. Bransford collector]. Günther, 1901 (1885-1902), p. 268.

Hyla rubra (part): Dunn and Emlen, 1932, p. 25.

Hyla dulcensis Taylor, 1958, p. 37 [holotype, K.U. No. 32168 from Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor collector].

DIAGNOSIS: From other species in the *Hyla rubra* group, *Hyla elaeochroa* can be distin-

guished by its medium size (snout-vent length of adult males, 26.3 to 37.7 mm.) and unpatterned posterior surfaces of the thighs; the latter character is shared with the smaller *staufferi* (snout-vent length of adult males, 20.6 to 29.0 mm.). *Hyla elaeochroa* is structurally similar to *rubra*, which differs by having bold brown or black reticulations on the posterior surfaces of the thighs. The other Middle American species in the *Hyla rubra* group (*boulengeri* and *rostrata*) differ from *elaeochroa* in larger size and by having black vertical bars on the posterior surfaces of the thighs. The combination of a long, protruding snout, vestigial webbing between the fingers, and greatly reduced webbing between the first and second toes distinguishes *elaeochroa* from other Middle American hylids.

DESCRIPTION: This is a medium-sized species of the *Hyla rubra* group; males attain a maximum snout-vent length of 37.7 mm., and females reach 40.3 mm. In a sample of 101 males from the Instituto Interamericano de

Ciencias Agrícolas at Turrialba, Cartago Province, Costa Rica, the snout-vent length is 28.1 to 35.0 (mean, 30.6) mm.; the ratio of tibia length to snout-vent length is 0.472 to 0.550 (mean, 0.505); the ratio of foot length to snout-vent length is 0.372 to 0.441 (mean, 0.408); the ratio of head length to snout-vent length is 0.321 to 0.372 (mean, 0.342); the ratio of head width to snout-vent length is 0.293 to 0.332 (mean, 0.309), and the ratio of the diameter of the tympanum to that of the eye is 0.444 to 0.683 (mean, 0.572). In 15 females from the same locality the snout-vent length is 31.9 to 35.7 (mean, 35.0) mm. The females differ from males in proportion only in the ratio of the diameter of the tympanum to that of the eye; in females this ratio is 0.493 to 0.645 (mean, 0.596). Specimens from the Golfo Dulce region in southeastern Costa Rica differ from those from the Caribbean lowlands by being larger and having relatively longer legs, longer head, and narrower head (table 19).

The head is slightly narrower than the body; the top of the head is barely convex. In dorsal profile, the snout is acutely rounded with a terminal point; in lateral profile, the snout is pointed and protruding beyond the edge of the lower jaw. The snout is long; the

nostrils are protuberant and situated at about four-fifths of the distance from the eyes to the tip of the snout. The canthus is rounded, but distinct. The loreal region is barely concave and inclined laterally; the lips are thin and moderately flared. A thin dermal fold extends posteriorly from the posterior corner of the eye above the tympanum to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and is separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and slender; an abbreviated axillary membrane is present. No dermal folds or tubercles are present on the ventrolateral edge of the forearm, but a weak transverse dermal fold is present on the wrist. The fingers are moderately long and slender. The terminal discs are large and somewhat truncate. The width of the disc on the third finger is slightly greater than the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercles on the first and fourth fingers are largest. The supernumerary tubercles are small, subconical, and indistinct in many specimens. The outer palmar tubercle is large and usually bifid; in some specimens it is par-

TABLE 19
Geographic Variation in Measurements and Proportions, with Means in Parentheses,
in Males of *Hyla elaeochroa* in Costa Rica.^a

Locality	N	Snout-vent Length	Tibia Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
Puerto Viejo	22	26.3-32.4 (29.7)	0.487-0.549 (0.520)	0.328-0.372 (0.352)	0.292-0.329 (0.308)	0.481-0.652 (0.568)
Batán, Limón, Suretka	26	26.3-32.7 (30.0)	0.471-0.539 (0.513)	0.323-0.379 (0.349)	0.300-0.342 (0.315)	0.444-0.621 (0.500)
Turrialba	101	28.1-35.0 (30.6)	0.472-0.550 (0.505)	0.321-0.372 (0.342)	0.293-0.332 (0.308)	0.444-0.683 (0.572)
Tilarán	21	28.8-33.6 (30.6)	0.473-0.544 (0.526)	0.314-0.361 (0.334)	0.284-0.319 (0.299)	0.483-0.652 (0.587)
Palmar Sur	13	29.4-35.1 (32.4)	0.482-0.538 (0.508)	0.331-0.372 (0.347)	0.300-0.347 (0.321)	0.473-0.619 (0.527)
Piedras Blancas	21	33.3-37.7 (35.2)	0.498-0.542 (0.511)	0.322-0.363 (0.344)	0.298-0.323 (0.313)	0.482-0.643 (0.573)
Rincón de Osa....	24	31.4-35.9 (34.1)	0.500-0.559 (0.531)	0.322-0.369 (0.351)	0.299-0.339 (0.319)	0.452-0.612 (0.541)

^a Based in part on data presented by León (1969).

tially tripartite. The prepollex is barely enlarged and in breeding males does not bear a nuptial excrescence. Only a vestige of a web is present between the fingers (fig. 68B). The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fifth the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A transverse dermal fold is present on the heel, but the tarsal fold is absent. The inner metatarsal tubercle is low, rounded, ovoid, and not visible from above. The outer metatarsal tubercle is elongate and distinct. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The sub-articular tubercles are moderately large and subconical. The supernumerary tubercles are small, conical, distinct, and present in a single row on proximal segments of each digit. The toes are about three-fourths webbed (fig. 69B). The webbing is absent between the first and second toes, except for a narrow fringe along the edge of the second toe; the web extends from the distal end of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed ventrally near the upper level of the thighs and is covered by a short, down-curved anal sheath. There are no anal tubercles. The skin on the belly and on the proximal posteroventral surfaces of the thighs is granular; elsewhere the skin is smooth, except that in some specimens small tubercles are present on the dorsum. These usually are not evident in preserved specimens. The tongue is cordiform, shallowly notched behind and barely free posteriorly. The dentigerous processes of the prevomers are transverse and situated between the moderately large, ovoid choanae. Some males lack teeth on one of the prevomerine processes. Other individuals have as many as eight teeth on one process; the total number of prevomerine teeth in 101 males from Turrialba, Cartago Province, Costa Rica, is three to 14 (mean, 9.9). In 15 females the total number of teeth varies from nine to 15 (mean, 11.8).

The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla elaeochroa* when active at night is pale yellow or yellowish tan with faintly darker dorsal markings (pl. 47, fig. 5). Some individuals when found by day were olive-green or tan with darker dorsal markings (pl. 47, fig. 6). In these specimens, the axillary region and edge of the throat often are pale bluish gray, whereas the belly is creamy white. In specimens that were active at night, the venter is pale yellow and the vocal sac is slightly darker yellow. The dorsal markings are highly variable. In some individuals, the spots are fused and aligned to form irregular longitudinal stripes. In other individuals, the spots are discreet and show no tendency toward a formation of stripes. In most individuals, a dark line extends from the tip of the snout through the nostril to the eye, and a dark interorbital triangular mark is present. The dorsal surfaces of the limbs are marked by brown transverse bands. Three to five bands are present each on the thigh, shank, and foot; two or three bands are present on the forearm. The iris is dull bronze with brown or gray suffusion, especially ventrally.

In preservative, the dorsum is pale yellowish tan, pale gray, or brown with darker markings. The anterior and posterior surfaces of the thighs are pale tan or creamy white. In many specimens the transverse marks on the limbs are not discernible in preservative. The dorsal markings are dull brown. The venter is creamy white.

León (1969, p. 526) discussed the geographic variation of color pattern in *Hyla elaeochroa* and stated: "In life, most individuals from the Pacific lowlands of Costa Rica are dark tan to greenish gray above with longitudinal stripes that are entire or broken, but some specimens (mostly males) are dusty brown or lack longitudinal stripes or interorbital triangle; females usually have the dark interorbital triangle and the stripes on the dorsum. Individuals from Turrialba, Cartago Province, Costa Rica, are pale olive-tan with olive-brown markings. Individuals from Puerto Viejo, Heredia Province, Costa Rica, are uniformly yellowish brown with or without

dark longitudinal stripes. Specimens from El Recreo, Zelaya Province, Nicaragua, are like those from Puerto Viejo. Males from Almirante, Bocas del Toro Province, Panamá, are pale brown with dark brown longitudinal stripes and an indistinct interorbital triangle. Females have a distinct interorbital triangle and dark brown blotches on the thighs and shanks."

TADPOLES: Large series of tadpoles in various developmental stages were obtained from a pond at Puerto Viejo, Heredia Province, Costa Rica. The growth and development of these tadpoles is summarized in table 20 and figure 75. Examination of figure 75 reveals that the most rapid growth takes place between stages 25 and 27 and again between stages 37 and 41.

A typical tadpole in developmental stage

27 has a body length of 7.2 mm. and a total length of 21.1 mm. The body is slightly deeper than wide; the snout is bluntly rounded in dorsal profile and more acutely rounded in lateral profile. The nostrils are large, directed anterodorsally, and situated about midway between the eyes and the tip of the snout. The eyes are moderately large and directed laterally. The spiracle is sinistral; the spiracular opening is below the midline at a point at about two-thirds the length of the body. The anal tube is short and dextral. The caudal musculature is thin and tapers posteriorly. At the midlength of the tail the depth of the musculature is less than that of either the dorsal or ventral fin. The dorsal fin extends onto the body. Terminally, both fins narrow to a thin tip (fig. 71B).

In life the dorsum is yellowish tan with

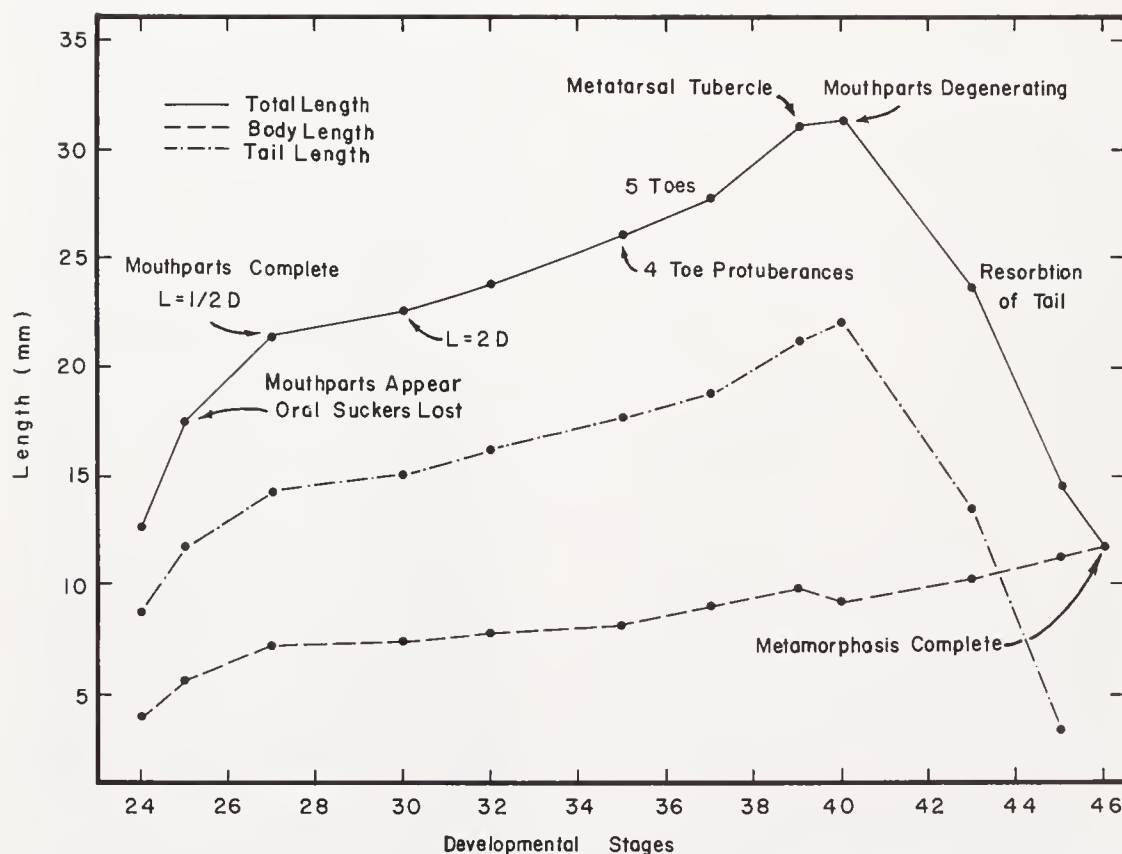


FIG. 75. Relative rate of growth in tadpoles of *Hyla elaeochroa* as correlated with developmental stages. Points are means of measurements given in table 20; formulas for the limb bud refer to its length (L) in relation to basal diameter (D).

TABLE 20
Measurements of Tadpoles, with Means in Parentheses, in Relation to Developmental Stages of *Hyla elaeochroa* from Puerto Viejo, Heredia Province, Costa Rica.^a

Stage	N	Body Length	Tail Length	Total Length
24	2	4.0	8.5- 9.0 (8.8)	12.5-13.0 (12.8)
25	64	5.0- 6.5 (5.7)	8.5-15.0 (11.8)	13.5-21.5 (17.6)
27	30	7.0- 7.5 (7.1)	13.0-16.0 (14.2)	20.0-23.0 (21.3)
30	15	7.0- 8.0 (7.3)	13.0-16.5 (15.0)	20.0-24.0 (22.4)
32	30	7.5- 8.5 (7.8)	15.0-17.0 (16.1)	22.5-25.0 (23.8)
35	35	8.0- 9.0 (8.1)	15.0-19.5 (17.7)	23.0-27.5 (25.9)
37	22	8.5- 9.5 (9.0)	16.0-22.0 (18.8)	25.0-31.0 (27.8)
39	14	9.5-10.5 (9.9)	19.0-24.9 (21.1)	28.5-33.5 (31.0)
40	27	7.0-11.5 (9.1)	15.0-23.0 (22.0)	23.0-34.5 (31.2)
43	10	8.0-12.0 (10.2)	11.0-17.0 (13.5)	20.0-26.0 (23.7)
45	16	10.0-12.0 (11.2)	1.0- 7.0 (3.4)	12.0-17.0 (14.6)
46	45	11.0-13.0 (11.8)	-----	-----

^a Data from León (1969).

grayish brown mottling. The belly and ventrolateral surfaces are white, except for some grayish brown mottling below the eye. The caudal musculature and fins are similarly pigmented with small grayish brown spots. The iris is gold with a small amount of orange peripherally in some specimens. In preservative the body and caudal musculature is pale tan. A dark brown line extends from the snout to the eye and thence posteriorly to the base of the caudal musculature. Brown flecks are scattered on the body, caudal musculature, and fins.

The mouth is small and anteroventral in position. Deep lateral folds are present in the lips. The median part of the upper lip is bare; the rest of the upper lip is fringed by one row of large papillae. Two or three rows are present on the lower limbs, and additional papillae are present in the lateral fold. The beaks are robust and bear fine serrations. The upper beak is in the form of an arch with long slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length and extend nearly to the lateral papillae. The second upper row is narrowly interrupted medially. The lower rows are complete and progressively shorter than the upper rows (fig. 72B).

MATING CALL: The call of *Hyla elaeochroa* consists of a series of short notes. Usually, individuals produce two to 15 notes in each

call group, but some individuals have been heard to produce call groups of 61, 75, 77, and 95 notes. The average number of notes per call group is 19. Call groups are produced at intervals of 1.5 to 48 seconds. The notes have a duration of about 0.17 of a second and pulse rate of about 42 pulses per second. The average fundamental frequency is 57 cycles per second; two harmonics are emphasized; the average of the lower emphasized harmonic is 1499 cycles per second and the average of the upper emphasized harmonic is 2911 cycles per second (table 17; pl. 26, fig. 1).

NATURAL HISTORY: *Hyla elaeochroa* inhabits humid lowland tropical forests where the frog apparently is active throughout the year. Males have been heard calling in every month except December. Mating seems to be dependent on heavy rainfall, which not only provides sufficient water in depressions to form temporary ponds, but apparently initiates the mating response on the part of the adults. Peaks of mating activity have been observed following heavy rains. At such times, large breeding congregations have been observed at Palmar and Piedras Blancas, Puntarenas Province, Costa Rica, at Tilarán, Guanacaste Province, Costa Rica, at Puerto Viejo, Heredia Province, Costa Rica, and at Turrialba, Cartago Province, Costa Rica.

Males usually call from emergent vegetation at the edge of ponds, but individuals also call from low bushes in and around the ponds.

The normal calling sites sometimes are forsaken in large choruses following heavy rains. At such times the sexual activity on the part of the males is such that the normal mating behavior patterns break down. An excellent example of this was observed at a small pond at Puerto Viejo, Heredia Province, Costa Rica, on the night of June 20, 1966 (pl. 10, fig. 1). Immediately following four hours of torrential rains, *Hyla elaeochroa* moved into the pond in great numbers. An estimated 3,000 frogs of this one species was present in a pond. Six calling males and two clasping pairs were observed on one *Monstera* leaf about 200 centimeters in diameter. In an estimated one square meter of herbs in shallow water, 27 calling males were present. Fifty-nine *Hyla elaeochroa* were observed on one stump approximately 1.5 meters in height and 70 cm. in diameter. Males were calling from the ground as well as while floating in the water. Succeeding nights at the same ponds, showed a decrease in the activity of this species and a resumption of normal sites and calling behavior (Duellman, 1967c, p. 175).

Duellman (1967a, p. 160) discussed the socialization in the call structure of *Hyla elaeochroa*. Observations made at La Lola, Limón Province, and at Palmar Sur, Puntarenas Province, Costa Rica showed that in small choruses (up to about 20 males) initial organization is present in the chorus structure. An apparent dominant individual initiates the chorus by producing a single pulsed note until joined by a second individual which also produces a single pulsed note. These call alternately until joined by a third frog, at which time the entire chorus begins calling with the regular series of short notes characteristic of the mating call. It is highly doubtful if such initial organization exists in large choruses, such as that observed at Puerto Viejo on June 20, 1966.

The eggs are deposited in mass in water adjacent to or adhering to floating vegetation. Hatchlings orient themselves vertically with the tip of the mouth to the surface of the water. They gradually sink to the bottom and then swim back to the surface again. Tadpoles in later stages of development (stage 25 and beyond) live in the shallow water near

the edges of the pond and hide in the vegetation. Metamorphosing young have been found from June through September. Forty-five recently metamorphosed individuals from Puerto Viejo have snout-vent lengths of 11.0 to 13.0 (mean, 11.8) mm.

REMARKS: Dunn and Emlen (1932, p. 25) considered *Hyla elaeochroa* and *quinquevittata* to be synonyms of *Hyla rubra*. Taylor (1952c, p. 859) regarded *quinquevittata* as a synonym of *elaeochroa*, which he considered to be distinct from *rubra*. Taylor (1958) described *Hyla dulcensis* from the Golfo Dulce region in southeastern Costa Rica. Duellman (1966b) after comparing adults, tadpoles, and mating calls of *dulcensis* and *elaeochroa*, concluded that a single species was involved. León (1969), reached the same conclusion.

ETYMOLOGY: The specific name *elaeochroa* is derived from the Greek *elaia*, meaning olive and the Greek *chroa*, meaning color of skin; the name obviously refers to the pale olive-colored dorsum.

DISTRIBUTION: *Hyla elaeochroa* inhabits the Caribbean lowlands from east-central Nicaragua to western Panamá and the Pacific lowlands of southeastern Costa Rica and extreme western Panamá (fig. 74). Most of the localities where the species has been collected are below 800 meters in elevation, but the species has been found at two localities above 1000 meters (El Silencio and Pacuare, Cartago Province) on the Caribbean slopes of the Cordillera de Talamanca, Costa Rica.

See Appendix 1 for the locality records of the 811 specimens examined.

Hyla staufferi Cope

Hyla staufferi Cope, 1865b, p. 195.

DIAGNOSIS: This small species is distinguished from other Middle American members of the *Hyla rubra* group by its small size (maximum snout-vent length in males, 29.0 mm., and in females, 31.6 mm.), presence of dark longitudinal markings on the body, and absence of markings on the thighs. These characters, plus the pointed protruding snout, vestigial webbing between the fingers, and reduced webbing between the first and second toes, distinguish *staufferi* from all other Middle American hylids.

CONTENT: Two subspecies are recognized: *Hyla s. staufferi* Cope inhabits subhumid lowlands from México to south-central Costa Rica, and *H. s. altae* Dunn occurs on the Pacific lowlands of western and central Panamá.

Minor differences in the ratio of tibia length to snout-vent length and in the ratio of the diameter of the tympanum to that of the eye exist throughout the range, but a trend is present from north to south for shorter snout-vent length, relatively shorter hindlimbs, and relatively smaller tympani (table 21). The primary difference between the subspecies is in the color pattern. In the Panamanian subspecies, the stripes on the dorsum are usually complete and the shanks are not barred, whereas in any given sample

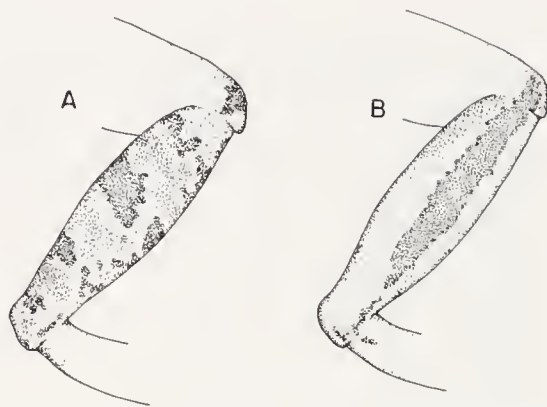


FIG. 76. Color pattern on the dorsal surface of the shank in *Hyla staufferi*. A. *H. s. staufferi*, K.U. No. 87081. B. *H. s. altae*, K.U. No. 77341. $\times 4$.

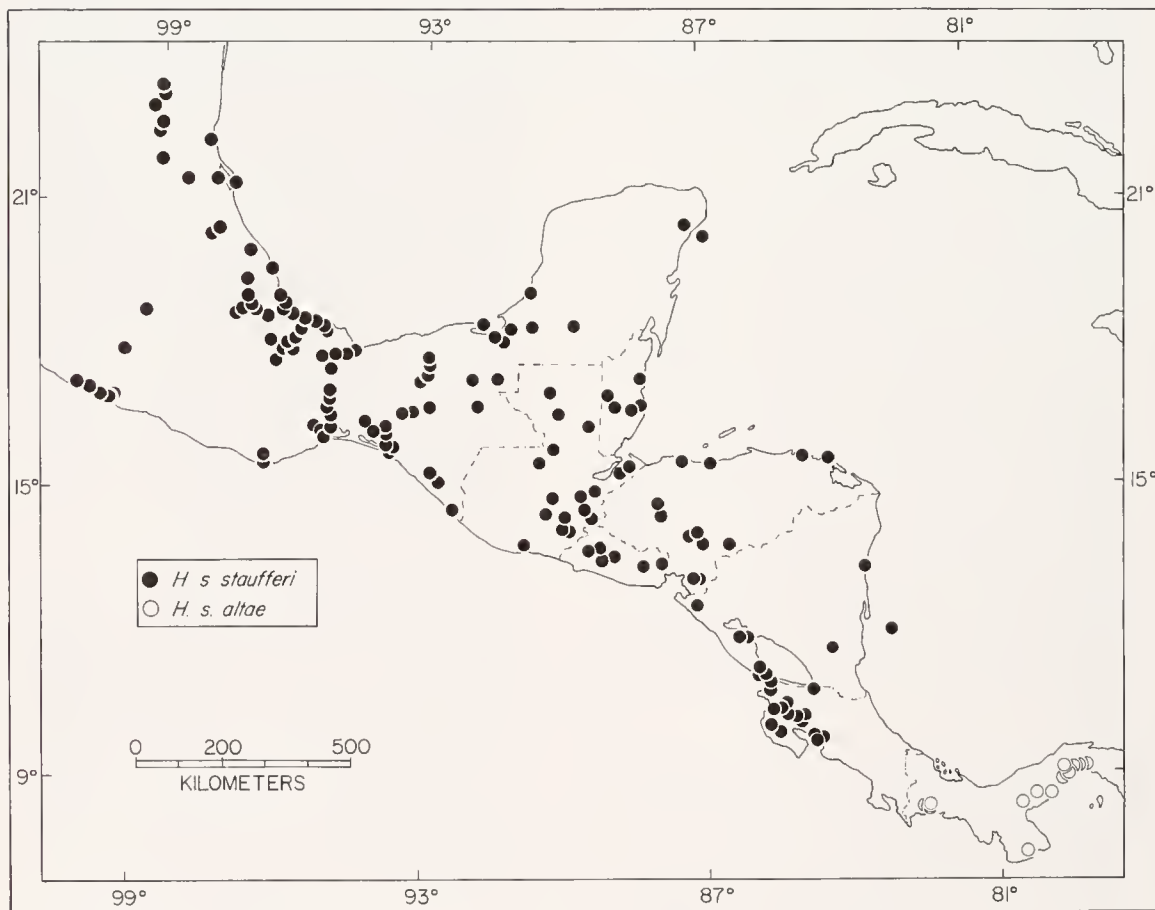


FIG. 77. Distribution of the subspecies of *Hyla staufferi*.

TABLE 21
Geographic Variation in Size, Proportions, and Color Pattern in Males of *Hyla staufferi*.^a
(Means are given in Parentheses)

Locality	N	Snout-vent Length (mm.)	Tibia Length/ S-V L	Tympanum/ Eye	Complete Dorsal Stripes (per cent)	Barred Shanks (per cent)
Veraeruz, México	47	23.0-27.3 (25.4)	0.460-0.519 (0.483)	0.482-0.678 (0.601)	0.0	100.0
Campeche, México	20	24.6-27.5 (25.5)	0.414-0.487 (0.458)	0.523-0.703 (0.615)	0.0	100.0
Oaxaca, México	29	24.3-28.7 (26.5)	0.432-0.499 (0.462)	0.524-0.759 (0.618)	9.3	100.0
Chiapas, México	20	23.2-27.8 (25.5)	0.421-0.499 (0.467)	0.600-0.750 (0.712)	10.0	100.0
El Petén, Guatemala ...	32	21.5-25.2 (23.5)	0.434-0.536 (0.490)	0.523-0.768 (0.627)	8.4	100.0
Jalapa, Guatemala	44	23.8-29.0 (26.9)	0.441-0.498 (0.471)	0.573-0.752 (0.672)	11.1	100.0
Esquipulas, Guatemala	18	21.1-27.2 (25.6)	0.444-0.526 (0.479)	0.553-0.761 (0.622)	3.9	100.0
San Salvador, El Salvador	31	24.7-28.6 (27.0)	0.442-0.517 (0.471)	0.484-0.697 (0.598)	0.0	100.0
Choluteca, Honduras ...	21	24.0-27.8 (26.4)	0.424-0.536 (0.478)	0.482-0.700 (0.599)	3.3	100.0
Chinandega, Nicaragua	18	23.0-27.2 (25.1)	0.480-0.535 (0.511)	0.547-0.702 (0.574)	0.0	100.0
Rivas, Nicaragua	35	21.5-26.8 (24.3)	0.461-0.529 (0.494)	0.484-0.749 (0.628)	3.0	92.7
Guanacaste, Costa Rica	54	20.7-26.6 (24.2)	0.448-0.510 (0.483)	0.481-0.672 (0.583)	5.5	98.1
Western Panamá	46	21.7-26.0 (23.7)	0.431-0.398 (0.454)	0.452-0.719 (0.567)	93.5	0.0
Central Panamá	26	22.2-25.8 (23.5)	0.413-0.472 (0.444)	0.498-0.583 (0.527)	96.3	0.0

^a Based in part on data presented by León (1969).

from Costa Rica northward no more than 11 per cent of the specimens have complete stripes on the dorsum and no fewer than 92 per cent have transverse bars on the shanks (fig. 76). Secondary differences exist in size and in the amount of webbing on the feet; in Panamanian specimens the toes are about two-fifths webbed, whereas in Costa Rica and northward the toes are about three-fourths webbed. Furthermore, minor differences exist in the mating calls; the duration of the notes is shorter and the major emphasized frequencies are higher in the Panamanian subspecies (table 17).

DISTRIBUTION: *Hyla staufferi* occurs at moderate and low elevations from southern Tamaulipas, México, to Nicaragua on the Caribbean versant and from Guerrero, México, to south-central Costa Rica on the Pacific versant, and on the Pacific lowlands of western and central Panamá (fig. 77).

Hyla staufferi staufferi Cope

Hyla staufferi Cope, 1865b, p. 195 [holotype, U.S.N.M. No. 15317 from Orizaba, Veracruz, México; Francis Sumichrast collector]. Brocchi, 1882, p. 36. Boulenger, 1882a, p. 400. Kellogg, 1932, p. 173. Smith and Taylor, 1948, p. 88. Stuart, 1963, p. 36.

Hyla eximia staufferi Cope, 1887, p. 14.

Hyla eximia (part): Günther, 1901 (1885-1902), p. 261.

Hyla culex Dunn and Emlen, 1932, p. 24 [holotype, M.C.Z. No. 16098 from Tela, Departamento Atlantidad, Honduras; Raymond A. Stadelman collector].

Hyla staufferi (part): Taylor, 1952c, p. 862. Duellman, 1966b, p. 274.

Hyla staufferi staufferi: León, 1969, p. 537.

DIAGNOSIS: *Hyla s. staufferi* differs from all other Middle American hylids by having an acuminate, protruding snout, transverse bars on the shanks, a dorsal pattern consisting of a dark triangular interorbital mark and interrupted longitudinal dark marks, and vestigial webbing on the hands. The subspecies *H. s. altae* differs by having complete longitudinal stripes on the dorsum and in lacking transverse bars on the shanks. *Hyla elaeochiroa* differs by being larger and in having a more irregular dorsal pattern, and *H. rubra* differs by having dark brown or black reticulations enclosing yellow spots on the posterior surfaces of the thighs.

DESCRIPTION: Males of this small subspecies attain a maximum snout-vent length of 29.0 mm., and females reach 31.6 mm. In a series of 29 males from the vicinity of Liberia, Guanacaste Province, Costa Rica, the snout-vent length is 20.7 to 26.1 (mean, 24.1) mm.; the ratio of tibia length to snout-vent length is 0.448 to 0.510 (mean, 0.488); the ratio of foot length to snout-vent length is 0.363 to 0.439 (mean, 0.398); the ratio of head length to snout-vent length is 0.313 to 0.368 (mean, 0.340); the ratio of head width to snout-vent length is 0.233 to 0.303 (mean, 0.275), and the ratio of the diameter of the tympanum to that of the eye is 0.481 to 0.667 (mean, 0.585). Seven females from the same locality have snout-vent lengths of 25.7 to 28.0 (mean, 26.6) mm. In proportions the females differ from the males only by having a slightly higher ratio of the diameter of the tympanum to that of the eye—0.482 to 0.706 (mean, 0.614). Specimens from farther north, particularly from Oaxaca, México, central Guatemala, and from El Salvador, are larger than those from the southern part of the range in Nicaragua and Costa Rica. Slight trends are apparent from north to south; the relative length of the tibia and the relative diameter of the tympanum decrease from

México southward to Costa Rica (table 21).

The head is no wider than the body; the top of the head is convex. In dorsal and lateral profiles, the snout is pointed; the snout projects beyond the leading edge of the lower jaw. The snout is long; the nostrils are barely protuberant and are situated at about four-fifths the distance from the eyes to the tip of the snout. The canthus is rounded and barely distinct; the loreal region is slightly concave, and the lips are thin and moderately flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and terminates at a point above the insertion of the arm. In some specimens, the dermal fold obscures the upper edge of the tympanum, which otherwise is distinct and is separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and slender; an abbreviated axillary membrane is present. There are no tubercles forming a row on the ventrolateral edge of the forearm, but a weak dermal fold is present on the wrist. The fingers are moderately short and stout and bear moderately large, barely truncate discs; the width of the disc on the third finger is about equal to the diameter of the tympanum. The subarticular tubercles are large and round; none are bifid. The supernumerary tubercles are small, subconical, and arranged in a single row on the proximal segment of each digit. The palmar tubercle is large, rounded, and bifid. The prepollex is barely enlarged; in breeding males it does not bear a nuptial excrescence. Webbing is essentially absent between fingers (fig. 68C). The hindlimbs are relatively short and robust; the heels of the adpressed limbs overlap by about one-fifth the length of the shank. The tibiotarsal articulation extends to the posterior edge of the orbit. A weak transverse dermal fold is present on the heel, but the tarsal fold is lacking. The inner metatarsal tubercle is moderately large, rounded, ovoid, and barely, if at all, visible from above. The outer metatarsal tubercle is small and conical. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately large and round. The supernumerary

tubercles are small, indistinct, or even absent in many specimens, and when present arranged in a single row on the proximal segment of the fourth and fifth digits; in some individuals faint supernumerary tubercles are evident on the second and third digits. The toes are about two-thirds webbed (fig. 69C). The webbing is vestigial between the first and second toes; it extends from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and from the distal end of the antepenultimate phalanx of the fourth to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the level of the upper edges of the thighs. A short, broad anal sheath is present; small tubercles are present below the anal opening. The skin on the belly and proximal posteroventral surfaces of the thighs is granular; elsewhere the skin is smooth. The tongue is ovoid, widest posteriorly, or cordiform with a shallow notch posteriorly. The dentigerous processes of the prevomers are transverse between the posterior margins of the elliptical choanae or are slightly posteromedially inclined. In the series of males from Liberia, one to six teeth are present on each prevomerine process; these specimens have a total of five to 11 (mean, 7.8) prevomerine teeth. In the females from the same locality, three to six teeth are present on each process, and the total number of prevomerine teeth is six to 11 (mean, 8.9). The vocal slits extend on the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla staufferi* is tan, olive-tan, or dull brown with irregular darker markings on the back and dorsal surfaces of the limbs (pl. 47, figs. 1 and 2). The dorsal markings usually consist of a dark interorbital spot and irregular longitudinal marks on the dorsum; in a few specimens from the southern part of the range the dorsal markings form distinct, continuous longitudinal stripes. Two or three dark transverse bars are present on each of the thigh, shank, and fore-

arm. A narrow dark brown line extends from the nostril to the eye and along the edge of the supratympanic fold. The flanks are creamy white or creamy tan, usually with dark brown or black flecks. The belly is creamy white, and the vocal sac in breeding males is dark yellow. The posterior surfaces of the thighs are dull brown. The iris is dull bronze with a heavy suffusion of brown.

In preservative the dorsum is pale tan or gray with brown markings. The posterior surfaces of the thighs are dull brown and the ventral surfaces are creamy tan.

TADPOLES: Small series of tadpoles in various developmental stages were reported on by Léon (1969). A typical tadpole in developmental stage 38 has a body length of 10.0 mm. and a total length of 28.2 mm. The body is deeper than wide. The snout is bluntly rounded in dorsal profile and deeply inclined anteroventrally in lateral profile. The nostrils are large, directed anterodorsally, and situated about midway between the eyes and the tip of the snout. The eyes are moderately large and directed laterally. The opening of the sinistral spiracle is directed posterodorsally at a point below the midline and at about two-thirds of the distance from the snout to the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is slender and tapers to a long point terminally. At midlength of the tail, the depth of the caudal musculature is much less than the depth of either the dorsal or ventral fins. The dorsal fin extends well onto the body, is deepest at midlength of the tail, and tapers to a shallow point posteriorly. The ventral fin has an equal depth on the anterior half of the tail and posteriorly tapers gradually to a terminal point (fig. 71C).

In life the body and caudal musculature is pale tan; dark brown reticulations are present on the tail. The caudal fins are transparent with pale pinkish orange tint ventrally. The belly is white, and the iris is pale gold. In preservative, the body and caudal musculature is pale creamy tan. Minute dark flecks are present on the dorsal surfaces of the body. Brown flecks and reticulations are present on the caudal musculature and fins. There is a

concentration of pigment on the edges of the fins.

The mouth is small, anteroventral, and has lateral folds in the lips. The median part of the upper lip is bare, and the rest of the upper lip bears a single row of moderately large papillae. Two rows of papillae are present on the lower lip, and additional papillae are present in the lateral fold. The beaks are moderately robust and bear small serrations. The upper beak is in the form of a broad arch with moderately long, slender lateral processes. The lower beak is V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length and extend to the labial papillae. The second upper row is narrowly interrupted medially. The first and second lower rows are equal in length and only slightly shorter than the upper rows; the third lower row is somewhat shorter. All lower rows are complete (fig. 72C).

MATING CALL: The mating call of *Hyla staufferi staufferi* consists of a series of short nasal notes, "ah-ah-ah-ah." The call groups are usually composed of two to 30 notes, but some individuals have been heard to produce 77 consecutive notes. The notes have a duration of 0.13 to 0.23 of a second and a pulse rate of 100 to 130 pulses per second. The fundamental frequency is at about 106 cycles per second. Two harmonics are emphasized with nearly equal intensity; these are at about 1743 and 3056 cycles per second (pl. 26, fig. 2; table 17).

NATURAL HISTORY: *Hyla staufferi staufferi* occurs in subhumid forests and savannas where rainfall is highly seasonal. Consequently, the frog is active for only a part of the year. During the dry season, individuals have been found in the axils of the leaves of elephant-ear plants and in bromeliads. Breeding activity begins with the onset of rains in May and June and continues until at least September.

Breeding takes place in shallow, temporary ponds. Males call from grasses, herbs, and low bushes at the edge of the pond. At some places after heavy rains, large numbers of *Hyla staufferi staufferi* congregate at breeding ponds. At these times the frogs evidently are in competition for calling sites, and the result is that some individuals call from the

ground or from shallow water. Eggs are deposited in small clumps in the shallow water.

The tadpoles develop in the shallow ponds, where they show a definite preference to areas containing dense grasses or aquatic vegetation. The tadpoles seek refuge amidst this vegetation.

One recently metamorphosed juvenile has a snout-vent length of 13.0 mm. The dorsum is dull olive-tan with no evidence of darker markings; the venter is creamy white.

REMARKS: Cope (1887, p. 14) considered *staufferi* to be a subspecies of *Hyla eximia*. Some other workers followed Cope who apparently concluded the relationship on the basis of the absence of webbing on the hand in both *staufferi* and *eximia*. Kellogg (1932, p. 174) concluded that *staufferi* and *eximia* were distinct species. Dunn and Emlen (1932, p. 24) named *Hyla culex* from Tela, Honduras on the basis of a single male (M.C.Z. No. 16098) and one female (U.S.N.M. No. 20267) from Patuca, Honduras. Most subsequent workers did not recognize *Hyla culex*. Duellman (1966b, p. 274) and León (1969, p. 537) considered *culex* to be a synonym of *Hyla staufferi*. On the basis of similarities in call structure, Blair (1960, p. 129) placed *Hyla staufferi* in the *Hyla eximia* group. Granted that similarities in the structure do exist, the morphological evidence overwhelmingly supports the inclusion of *Hyla staufferi* in the *Hyla rubra* group, which is only distantly related to the *Hyla eximia* group.

The proclivity of *Hyla staufferi* for subhumid environments has permitted its dispersal throughout most of northern Middle America. Extensive areas of humid lowland tropical forest apparently are barriers to this frog. In the lowland area of El Petén, Guatemala, *Hyla staufferi staufferi* inhabits the open savannas, but is absent from the main forest.

ETYMOLOGY: The specific name *staufferi* obviously is a patronym. I have been unable to determine the identity of Mr. Stauffer.

DISTRIBUTION: *Hyla staufferi staufferi* inhabits savannas and subhumid forests in the lowlands to moderate elevations from southern Tamaulipas, México, southward to Nicaragua on the Caribbean versant and from Guerrero, México to northwestern Costa Rica

on the Pacific (fig. 77). In parts of northern-central America, the range apparently is discontinuous. The subspecies occurs in islands of savannas surrounded by rain forests in northern Guatemala; it occurs in subhumid valleys in Guatemala and Honduras.

See Appendix I for the locality records of the 1973 specimens examined.

Hyla staufferi altae Dunn

Hyla altae Dunn, 1933, p. 61 [holotype, M.C.Z. No. 17972 from Summit, Canal Zone, Panama; Emmett R. Dunn collector].

Hyla staufferi (part): Taylor, 1952c, p. 862. Duellman, 1966b, p. 274.

Hyla staufferi altae: León, 1969, p. 540.

DIAGNOSIS: *Hyla staufferi altae* differs from all other Middle American hylids by having an acuminate, protruding snout, vestigial webbing on the hands, no transverse bars on the shanks, and a dorsal pattern consisting of a dark triangular interorbital mark and complete longitudinal dark stripes. The nominate subspecies differs by having incomplete longitudinal marks on the dorsum and transverse bars on the shanks. *Hyla elaeochroa* differs by being larger and in having an irregular dorsal pattern, and *H. rubra* differs by having dark brown or black reticulations enclosing yellow spots on the posterior surfaces of the thighs.

DESCRIPTION: Males of this small subspecies attain a maximum snout-vent length of 26.0 mm., and females reach 27.8 mm. In a series of 29 males from the Pacific lowlands between the Canal Zone and Chepo, Panamá, the snout-vent length is 22.2 to 25.8 (mean, 23.5) mm.; the ratio of tibia length to snout-vent length is 0.413 to 0.472 (mean, 0.444); the ratio of foot length to snout-vent length is 0.352 to 0.399 (mean, 0.380); the ratio of head length to snout-vent length is 0.313 to 0.341 (mean, 0.327); the ratio of head width to snout-vent length is 0.262 to 0.302 (mean, 0.279), and the ratio of the diameter of the tympanum to that of the eye is 0.498 to 0.583 (mean, 0.527). Three females from the same area have snout-vent lengths of 26.8 to 27.8 (mean, 27.1) mm. They show no significant differences in proportions from the males. Comparison of these specimens from central Panamá with specimens from western Pan-

amá reveal that the latter are slightly larger and have slightly longer legs and larger tympani (table 21).

Structurally, *Hyla staufferi altae* is like the nominate subspecies; the reader is referred to the account of *Hyla staufferi staufferi* for a detailed description. The only noticeable structural difference is in the amount of webbing on the foot. In *H. s. altae* the toes are slightly more than one-half webbed. Webbing is vestigial between the first and second and between the second and third toes. The web extends from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and from the middle of the antepenultimate phalanx of the fourth to the middle of the penultimate phalanx of the fifth toe.

The general coloration of *Hyla staufferi altae* at night is yellowish or olive-tan with brown longitudinal markings (pl. 47, fig. 3). By day, the frogs are grayish tan or olive-gray with brown markings. The posterior surfaces of the thighs are colored like the dorsum. The venter is white; the vocal sac in breeding males is yellow. A pair of distinct, usually complete, dark brown dorsolateral stripes and a pair of entire paravertebral stripes are invariably present. In some specimens, a narrow vertebral stripe is present. A longitudinal dark brown stripe is present on the dorsal surface of the shank. A faint interorbital spot or transverse bar is present in some specimens. The iris is dull bronze with dark brown suffusion and reticulations.

In preservative, the dorsum is tan or grayish brown with dark brown markings. The ventral surfaces are creamy tan.

TADPOLES: The size and structure of the tadpoles of *Hyla staufferi altae* are like those of the nominate subspecies. The coloration is somewhat paler. In life the dorsum is tan, and the venter is a pale golden white. The caudal musculature is pale creamy tan, and the caudal fins are transparent. Minute dark brown or black flecks are present on the tail. The iris is pale bronze.

MATING CALL: The call of *Hyla staufferi altae* is like that of the nominate subspecies, except the notes are slightly shorter and that the lower emphasized harmonic is at a point

about 300 cycles per second higher than in the nominate subspecies (table 17).

NATURAL HISTORY: This subspecies occurs in xeric, scrubby forests and in savannas. The breeding season coincides with the rains, which usually begin in May and last until October. Males call from grasses and herbs in or at the edge of temporary ponds. The tadpoles have been found in shallow grassy ponds, where they seek refuge among the vegetation.

REMARKS: Taylor (1952c, p. 863) and Duellman (1966b, p. 274) did not recognize *altae*. Both of these workers considered *Hyla staufferi* to be monotypic. León (1969, p. 533) demonstrated the minor structural differences between Panamanian and more northern populations of *Hyla staufferi*, and he pointed out the distinctive color pattern of the Panamanian population. At the present time, no specimens representing an intergrading between the subspecies are available. Slight clinal variation in size and certain proportions is evident throughout the range of the species (table 21). The distinctive break in coloration occurs at a hiatus in the distribution, namely the humid Golfo Dulce in southeastern Costa Rica, where *Hyla staufferi* does not occur.

ETYMOLOGY: The subspecific name is a patronym for Alta Merle Dunn.

DISTRIBUTION: *Hyla staufferi altae* occurs on the subhumid Pacific lowlands of Panamá from Concepción, Chiriquí Province, to Chepo in the lower Bayano valley, Panamá Province (fig. 77).

See Appendix 1 for the locality records of the 154 specimens examined.

Hyla boulengeri (Cope)

Scytotis boulengeri Cope, 1887, p. 12 [holotype, U.S.N.M. No. 13974 from "Nicaragua"; J. A. McNeil collector].

Hyla boulengeri: Günther, 1901 (1885-1902), p. 267. Taylor, 1952c, p. 856. León, 1969, p. 511.

DIAGNOSIS: *Hyla boulengeri* is a medium-sized species having an acuminate snout, tuberculate dorsum, no webbing on the hand, and a bold contrasting pattern of black and yellow or green vertical bars on the thighs. The only Middle American hyliid with which it can be confused is *Hyla rostrata*, which has

a more pointed snout, smooth dorsum, vestigial webbing on the hand, a creamy white groin and a brown or gray vocal sac. *Hyla boulengeri* usually has a dark spot in the groin and a white vocal sac. Furthermore, the pale bars on the thighs in *rostrata* are pale orange in life. The only other Middle American hyliid having black and yellow vertical bars on the thighs in *Hyla lancasteri*, which has a short, truncate snout and webbing between the fingers. The long unwebbed fingers and truncate discs of *Hyla boulengeri* are like those of many species of *Eleutherodactylus*.

DESCRIPTION: This is the largest Middle American species in the *Hyla rubra* group. Males attain a maximum snout-vent length of 48.7 mm., and females reach 52.8 mm. In a series of 25 males from Puerto Viejo, Heredia Province, Costa Rica, the snout-vent length is 37.5 to 42.9 (mean, 41.6) mm.; the ratio of tibia length to snout-vent length is 0.512 to 0.620 (mean, 0.552); the ratio of foot length to snout-vent length is 0.380 to 0.462 (mean, 0.431); the ratio of head length to snout-vent length is 0.361 to 0.412 (mean, 0.383); the ratio of head width to snout-vent length is 0.314 to 0.359 (mean, 0.341), and the ratio of the diameter of the tympanum to that of the eye is 0.630 to 0.789 (mean, 0.713). Eight females from the same locality have snout-vent lengths of 44.8 to 52.8 (mean, 49.4) mm. The ratio of the diameter of the tympanum to that of the eye is 0.708 to 0.800 (mean, 0.769); no other sexual dimorphism in proportions is evident. No noticeable geographic variation in size and proportion occurs in Middle America; however, specimens currently assigned to *Hyla boulengeri* from the Pacific lowlands of northwestern South America are noticeably smaller.

The head is longer than wide; the top of the head is slightly convex. In lateral and dorsal profiles, the snout is acuminate; the tip of the snout projects beyond the leading edge of the lower jaw. The snout is long; the nostrils are greatly protuberant, directed dorso-laterally, and situated just above the leading edge of the lower jaw at a point about four-fifths from the eyes to the tip of the snout. The canthus is rounded and barely distinct; the loreal region is flat and inclined laterally. The lips are flared. A thin dermal fold extends

posteriorly from the posterior edge of the eye, above the tympanum, and thence downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is posteroventral to the eye and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arm is moderately long and slender; no axillary membrane is present. There are no tubercles forming a row along the ventrolateral edge of the forearm, nor is a transverse fold present on the wrist. The fingers are long and slender and bear large truncate discs; the width of the disc on the third finger is about equal to the diameter of the tympanum. Narrow dermal fringes are present on the edges of the digits. The subarticular tubercles are large and round; none is bifid. Small, conical supernumerary tubercles are present on the proximal segments of each digit. The palmar tubercle is large, flat, and tripartite. An elongate, flat, tubercle is present on the prepollex, which is barely enlarged and does not bear nuptial excrescences in breeding males. Webbing is absent between the fingers (fig. 68D). The hindlimbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to a point between the eye and the nostril. One or two tubercles and a thin transverse dermal fold are present on the heel. A weak tarsal fold is present. The inner metatarsal tubercle is low, flat, round, and not visible from above. The outer metatarsal tubercle, if present, is small and conical. The toes are long and slender and bear discs that are truncate and nearly as large as those on the fingers. The subarticular tubercles are large and round; the supernumerary tubercles are small, round, and arranged in a single row on the proximal segment of each digit. The toes are about three-fourths webbed (fig. 69D). The webbing exists as a fringe on the medial side of the first toe and the lateral edge of the second toe; the webbing extends from the base of the disc of the second to the base of the penultimate phalanx of the third; from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the fifth toe.

The anal opening is directed posteroventrally at a level at the middle of the thighs. The anal sheath is short and broad. The skin on the belly and proximal posteroventral surfaces of the thighs is granular; that on the ventral surfaces of the limbs is smooth. On all of the dorsal surfaces, the skin bears small tubercles. The tongue is narrowly cordiform, shallowly notched behind, and barely free posteriorly. The dentigerous processes of the prevomers are closely approximated transverse ridges between the middle of the elongate, elliptical, large, choanae. In the series of males from Puerto Viejo, three to 10 teeth are present on each process, and a total number of prevomerine teeth is eight to 17 (mean, 13.0). In the eight females six to 10 teeth are present on each process, and the total number of prevomerine teeth is 12 to 19 (mean, 15.2). The vocal slits extend from the midlateral base of the tongue to the angle of the jaw. The vocal sac is single, median, subgular, and moderately distensible.

In some specimens, the dark colored interorbital triangular mark is bordered by a row of tubercles. Also, rugosities are present on the tip of the snout, edge of the eyelid, edge of the lower jaw, and ventrolateral edges of the forearm and tarsus in some specimens. Individuals from the Caribbean lowlands of Central America generally are less tuberculate than those from the Golfo Dulce region in Costa Rica.

The general coloration of *Hyla Boulengeri* is grayish tan or a dull green with darker dorsal markings (pl. 48, figs. 1 and 2). Individuals from Puerto Viejo, Heredia Province, Costa Rica, when calling at night were grayish tan with slightly darker dorsal markings. The flash colors on the flanks are a pale yellowish green. By day, the dorsum was brown or tan with dark brown markings. The venter is creamy white; gray flecks were present on the throat. The groin was pale green with black spots or mottling. The anterior and posterior surfaces of the thighs and the inner edges of the tarsi were greenish yellow to orange-yellow with black bars. The iris was dull bronze. The dorsal markings normally consist of a dark interorbital triangular mark and two or more large dark blotches on the dorsum. Three or four transverse brown bars

are present on the dorsal surfaces of the thighs; two or three bars are present each on the shank, foot, and forearm. The anterior and posterior surfaces of the thighs have long, vertical black bars, separated by pale green, yellowish green, or yellow-orange interspaces. Short bars are present on the inner surfaces of the feet; these likewise are separated by pale green or yellow interspaces. The groin is pale yellow, greenish yellow, or cream-colored. The groin is variously marked by black mottling, one large black spot, or two or three smaller black spots.

In preservative the dorsum is dull brown with darker brown markings. The interorbital triangle is apparent. The anterior and posterior surfaces of the thighs and the intersurfaces of the tarsi are creamy white with black bars. The venter is pale cream; brown flecks are present on the throat.

TADPOLES: A small series of tadpoles in later developmental stages is available; the sizes of these specimens were discussed by León (1969, p. 516). A tadpole in developmental stage 30 had a body length of 11.0 mm. and a total length of 33.2 mm. The largest individuals are in developmental stage 42; one such tadpole has a body length of 13.0 mm. and a total length of 34.0 mm. A typical tadpole in developmental stage 38 has a body length of 11.5 mm. and a total length of 33.5 mm. The body is slightly deeper than wide. The snout is bluntly rounded in dorsal profile and inclined anteroventrally, but rounded terminally, in lateral profile. The nostrils are small, directed anterolaterally, and slightly closer to the eyes than to the tip of the snout. The eyes are moderately large and directed laterally. The spiracle is sinistral; its opening is directed posteriorly at a point below the midline and about two thirds the distance from the snout to the posterior edge of the body. The cloacal tube is short and dextral. The caudal musculature is moderately shallow and gradually tapers posteriorly. The caudal fins are deep; at midlength of the tail the caudal musculature is shallower than either the dorsal or ventral fin. The dorsal fin extends onto the body nearly to the posterior edge of the eye; both fins are deepest just anterior to the midlength of the tail and both

taper rather sharply to a terminal point (fig. 71D).

In life the body is silvery yellow; the caudal musculature is pale cream, and the fins are transparent. The tail is marked by large, closely spaced black spots on the middle two-thirds of its length. In preservative, the tadpoles lack pigment except for the spots on the tail.

The mouth is small and anteroventral in position. Shallow lateral folds are present in the lips. The lips lack papillae, except laterally, where there is a single row of large, blunt papillae. Medial to these, in the lateral fold, there are numerous, small conical papillae. The beaks are massive and bear long pointed serrations. The upper beak forms a narrow arch with moderately long lateral processes. The lower beak is shallowly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length and extend to the lip. In all specimens, the second upper row is narrowly interrupted medially, whereas the first upper row usually is complete. The first and second lower rows are about equal in length, usually complete, and much shorter than the upper rows. The third lower row is very short and gives the appearance of being a modified part of the lower lip. The teeth are long, slender, and curved; they are especially large in the third lower row (fig. 72D).

MATING CALL: The call of *Hyla boulengeri* consists of a single, low-pitched note, which might be described as a low "growl." Notes are repeated at intervals of 10 seconds to several minutes. The notes have a duration of 0.24 to 0.47 of a second and a pulse rate of 80 to 120 pulses per second. The fundamental frequency is at about 71 cycles per second. Two harmonics are emphasized with nearly equal intensity; these are at about 1600 and 2800 cycles per second (table 17; pl. 27, fig. 2).

NATURAL HISTORY: This species inhabits humid, lowland tropical forests with rainfall rather equally distributed throughout the year, consequently, the frogs are active throughout most of the year. The breeding season apparently is lengthy, because calling males have been heard in every month from January through November. Males call from secluded

positions. Normal calling sites include stumps or logs that are covered with broad-leaved vegetation, under which the frogs perch. Other individuals have been found calling from dense bushes, or depressions in logs or stumps in and at the edge of ponds. Amplexus takes place out of the water. Eggs are deposited in shallow water. No information is available concerning early developmental stages of the tadpoles, but tadpoles in advanced stages of development were found in a temporary pond at Rincón de Osa, Puntarenas Province, Costa Rica.

A recently metamorphosed young from Rincón de Osa, Puntarenas Province, Costa Rica, has a snout-vent length of 15.0 mm. The head is as long as wide, and the eyes are prominent. The limbs are weakly barred, and the skin is rugose above and granular below. The dorsum and limbs are pale green (change to gray-brown in preservative), and the venter is white. The interorbital space, supratympanic fold, and scapular region are darker than the rest of the body. The fingers lack

webs, and the webbing on the foot is the same as in the adults. Small metatarsal tubercles are present, but the tarsal fold is absent.

REMARKS: Dunn and Emlen (1932, p. 25) placed *Hyla lancasteri* Barbour in the synonymy of *Hyla Boulengeri*. Taylor (1952c) followed Dunn and Emlen with reservation and described *Hyla moraviaensis* from eastern Costa Rica. Duellman (1966b, p. 271) showed that *Hyla lancasteri* was not the same as *Hyla Boulengeri* and that *Hyla moraviaensis* was a synonym of *Hyla lancasteri*.

ETYMOLOGY: The specific name is a patronym for the famous Nineteenth Century herpetologist George Albert Boulenger.

DISTRIBUTION: In Central America, *Hyla Boulengeri* occurs on the Caribbean lowlands from central Nicaragua to South America where it ranges on the Pacific lowlands to northwestern Ecuador. This species also occurs in locally humid areas in Guanacaste Province, and in the humid Golfo Dulce region of Costa Rica (fig. 78). *Hyla Boulengeri* has

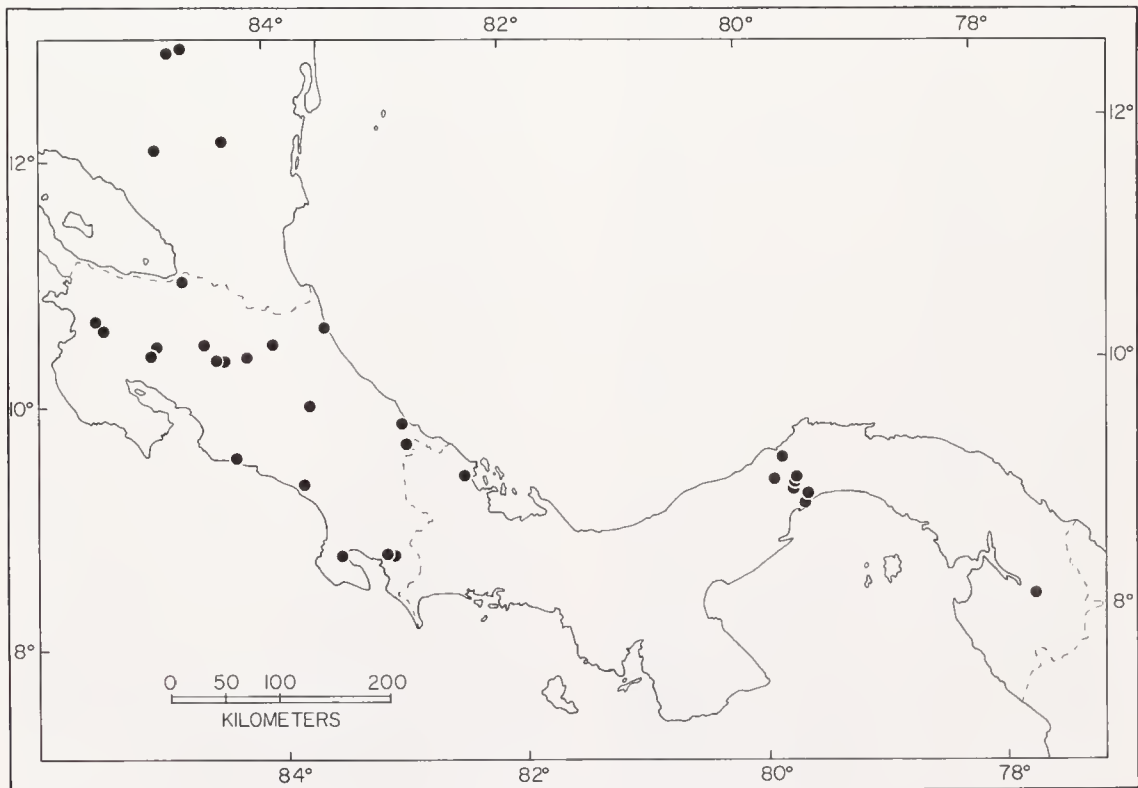


FIG. 78. Distribution of *Hyla Boulengeri*.

been found at elevations of 620 meters at Turrialba, Cartago Province, and at 700 meters at Tilarán, Guanacaste Province, Costa Rica.

See Appendix 1 for the locality records of the 178 specimens examined.

Hyla rostrata Peters

Hyla rostrata Peters, 1863, p. 466 [holotype, Z.M.B. No. 3175 from Caracas, Venezuela; Golmer collector]. Rivero, 1968, p. 133.

Hyla foliamorta Fouquette, 1958, p. 125 [holotype, T.N.H.C. No. 23109 from 11 kilometers north of Miraflores Locks, Canal Zone, Panamá; M. J. Fouquette, Jr. collector]. León, 1969, p. 520.

DIAGNOSIS: *Hyla rostrata* is a medium-sized species having an acuminate and protruding snout, smooth dorsum, vestigial webbing on the hand, a dark gray or brown vocal sac, and orange and black bars on the thighs. This species resembles *H. Boulengeri*, which lacks webbing on the hand and has a tuberculate dorsum, white vocal sac, and black and yellow or green bars on the thighs. *Hyla rostrata* can be confused with no other Middle American hylids.

DESCRIPTION: This is a moderately large member of the *Hyla rubra* group. Males attain a maximum snout-vent length of 45.7 mm. The one female from Central America has a snout-vent length of 41.0 mm. In a series of 28 males from an area between Tocumen and Chepo, Panamá Province, Panamá, the snout-vent length is 40.0 to 45.7 (mean, 42.5) mm.; the ratio of tibia length to snout-vent length is 0.541 to 0.609 (mean, 0.572); the ratio of foot length to snout-vent length is 0.403 to 0.461 (mean, 0.432); the ratio of head length to snout-vent length is 0.352 to 0.397 (mean, 0.371); the ratio of head width to snout-vent length is 0.302 to 0.354 (mean, 0.323), and the ratio of the diameter of the tympanum to that of the eye is 0.563 to 0.811 (mean, 0.672).

The head is as wide as the body and somewhat longer than wide. The snout is acuminate in dorsal and lateral profiles; in lateral profile, the snout projects well beyond the leading edge of the lower jaw. The snout is long; the nostrils are protuberant, directed dorsolaterally, and situated at about four-fifths the distance from the eyes to the tip of the snout, slightly anterior to the leading

edge of the lower jaw. The canthus is rounded and barely discernible; the loreal region is flat and inclined laterally and confluent with the slightly flared lips. A moderately heavy dermal fold extends from the eye above the tympanum and thence downward to a point above the insertion of the arm. The fold barely obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and slender; there is no axillary membrane. Tubercles are absent from the outer edge of the forearm, and there is no transverse fold on the wrist. The fingers are long and slender and bear large truncate discs; the width of the disc on the third finger is greater than the diameter of the tympanum. The subarticular tubercles are very large and round. The supernumerary tubercles are low, indistinct, and irregular in position. The palmar tubercle is low and flat basally and higher and bifid distally. A low, ovoid tubercle is present on the prepollex, which is barely enlarged, and in breeding males does not bear a nuptial excrescence. A vestige of a web exists between the fingers (fig. 68E). The legs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the nostril. A heavy transverse dermal fold is present on the heel, but a tarsal fold is absent. The inner metatarsal tubercle is small, ovoid, subconical, and not visible from above. The outer metatarsal tubercle is slightly smaller and conical. The toes are long and slender and bear discs that are somewhat smaller than those on the hands. The subarticular tubercles are large and round, and the supernumerary tubercles are small, subconical, and arranged in a single row on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 69E). The webbing is vestigial between the first and second toes, except for a fringe on the lateral edge of the second toe; the webbing extends from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the level of the upper edges of the thighs; a short anal sheath is present. The skin on the belly and proximal posteroventral surfaces of the thighs is granular; elsewhere the skin is smooth. The tongue is cordiform, moderately notched behind but barely free posteriorly. The dentigerous processes of the prevomers are transverse between the moderately large, elongately elliptical choanae. There are four to nine teeth on each process; the total number of prevomerine teeth is nine to 15 (mean, 11.2). The vocal slits extend from the midlateral base of the tongue to the angle of the jaw. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla rostrata* is gray or tan with darker dorsal markings (pl. 48, fig. 3). The dorsal ground color is pale tan to grayish tan or reddish tan with darker brown markings. The markings consist of a distinctive interorbital bar, usually triangular in shape with the apex directed posteriorly. The rest of the dorsum is marked by two irregular blotches or broad reticulations. In some individuals, the dark marks are narrowly outlined by pale gray. Narrow transverse bars are present on the dorsal surfaces of the limbs. The groin is creamy white without dark spots or mottling. The anterior and posterior surfaces of the thighs are yellow or orange with black or dark brown markings. Usually these markings are in the form of broad, vertical bars, but in some individuals the bars are interconnected or have a pale center. The belly is white, and the vocal sac is dark gray or brown. The iris is pale bronze.

In preservative, the dorsum is pale gray or pale brown with darker gray or brown markings, which in most specimens are narrowly outlined with creamy tan. The anterior and posterior surfaces of the thighs are creamy white with dark brown markings. The venter is creamy white except for the throat which is grayish brown.

TADPOLES: A typical tadpole in developmental stage 34 had a body length of 9.5 mm. and a total length of 34.5 mm. The body is slightly deeper than wide. In dorsal profile the snout is bluntly rounded; in lateral profile the snout slopes acutely from the nostrils to terminate in a truncate tip. The nostrils are

protuberant and about midway between the eyes and the tip of the snout. The eyes are moderately large and directed laterally. The sinistral spiracle has its opening directed posteriorly below the midline at a point about two-thirds of the distance from the snout to the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is relatively shallow and is finely tapered posteriorly. At midlength of the tail, the depth of the musculature is equal to about two-thirds of either the depth of the dorsal or the ventral fin. The dorsal fin extends well onto the body, nearly to the posterior edge of the eye, and terminates distally in a narrow fringe along the musculature. The ventral fin has an equal depth throughout the anterior half of the tail and then diminishes to a narrow fringe along the musculature, thereby resulting in a xiphicercal tail (fig. 71E).

In life the body and tail are pale greenish yellow with black spots; the iris is pale gold. In preservative, the dorsal part of the body and the snout anterior to the eyes is dark brown. The rest of the body lacks pigment, except for a few small flecks below the eye. The caudal musculature is creamy white and the fins are transparent. Both are marked by spots of large pigment, larger spots made up of smaller pigment, and dark reticulations.

The mouth is small and anteroventral. The lips have a shallow lateral fold. The median part of the upper lip is bare, and the rest of the lips are bordered by a single row of moderately large, blunt papillae. Additional small papillae are present in the lateral fold. The beaks are robust and bear moderately long serrations. The upper beak forms a broad arch with long, slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are about equal in length and extend nearly to the lips; the second upper row is narrowly interrupted medially. The lower rows are shorter than the upper rows and the third row is the shortest. In some specimens, the first lower row is narrowly interrupted medially. The teeth are not exceptionally long nor are they curved. The longest teeth are in the first upper row (fig. 72E).

MATING CALL: The call of *Hyla rostrata* is a single, low-pitched note. The call repe-

tition rate varies from about 20 seconds to several minutes. The duration of the note is from 0.23 to 0.86 of a second, and the pulse rate is 50 to 60 pulses per second. The fundamental frequency is at about 56 cycles per second. Two harmonics are emphasized with nearly equal intensity; one of these is at about 920 cycles per second, and the other is at about 3055 cycles per second (table 17; pl. 27, fig. 3).

NATURAL HISTORY: *Hyla rostrata* inhabits subhumid, scrubby forest and savannas, which have a relatively short rainy season usually extending from May to September. This species breeds in temporary ponds in the savannas and scrub forests. Fouquette (1958, p. 128) stated that males call from "about four

to seven feet above the ground in tall cane grasses or small ponds." In the area between Tocumen and Chepo, Panamá Province, Panamá, this species has been observed to call from low, dense, sometimes thorny, bushes in and at the edge of temporary ponds. The tadpoles were found in a weedy temporary pond; the tadpoles sought refuge in the vegetation.

On the Pacific side of the Canal Zone, *Hyla rostrata* occurs sympatrically with *Hyla boulengeri*, which, according to Fouquette (1958, p. 128) calls from lower sites. Throughout most of the range of *rostrata*, *boulengeri* is absent. Apparently *Hyla rostrata* replaces *boulengeri* in the more xeric habitats.

REMARKS: Fouquette (1958) recognized this species as distinct from *boulengeri* in Pan-

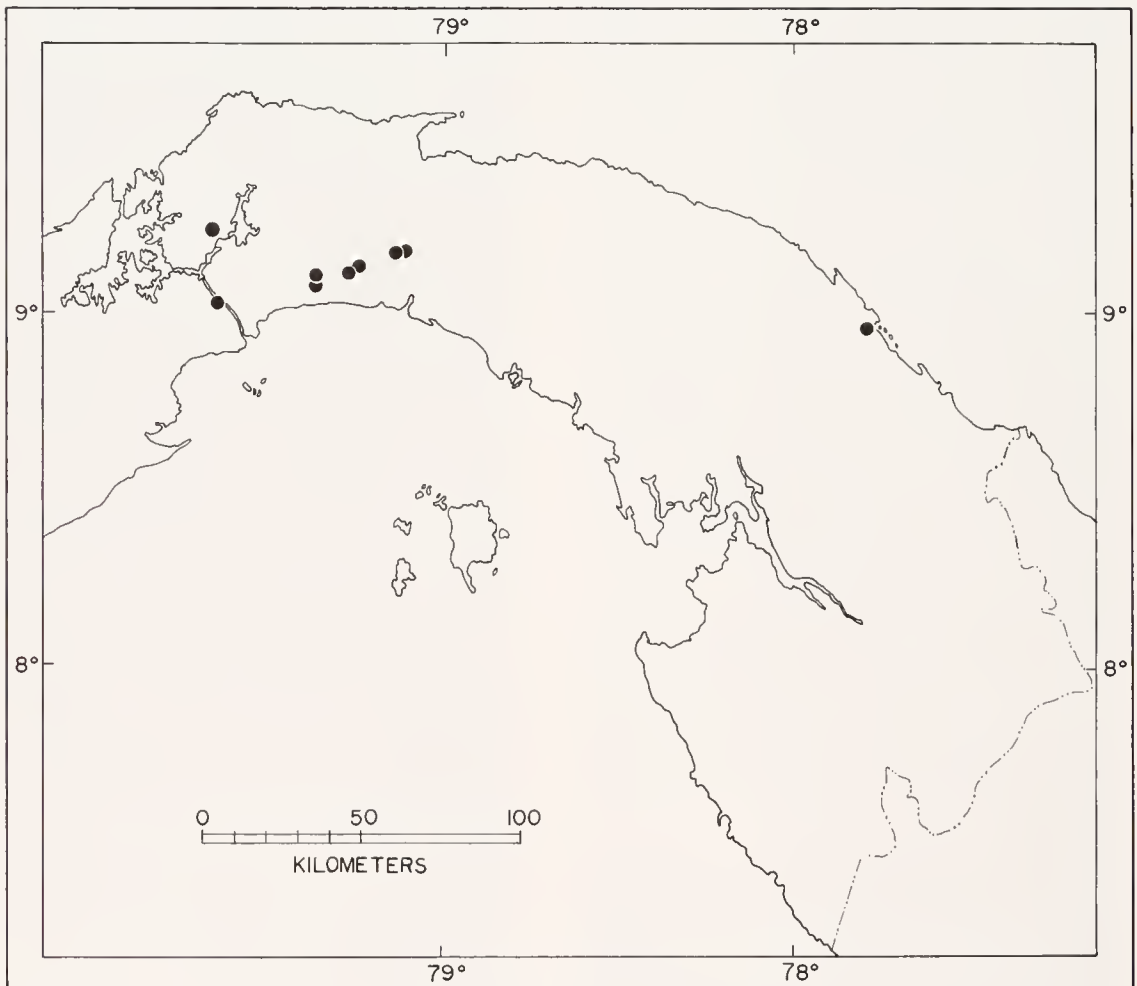


FIG. 79. Distribution of *Hyla rostrata*.

amá and named *Hyla foliamorta*. Rivero (1968) showed that *Hyla rostrata* Peters was the earliest available name for the species.

ETYMOLOGY: The specific name is derived from the Latin *rostrum* meaning muzzle and refers to the prominent snout.

DISTRIBUTION: *Hyla rostrata* occurs in sub-humid habitats from central Panamá eastward to northern Colombia, northern Venezuela, and the Guianas (fig. 79).

See Appendix 1 for the locality records of the 50 specimens examined.

The *Hyla microcephala* Group

DEFINITION: The members of this group are small species; males attain a maximum snout-vent length of 27 mm. and females, 32 mm. The dorsum is yellowish tan with brown markings; the thighs are uniformly yellow. The palpebral membrane is clear. The fingers are about one-third, and the toes about three-fourths webbed. Dermal folds and appendages are lacking on the limbs, but a distinct axillary membrane is present. Males have single, median, subgular vocal sacs, but lack nuptial excrescences on the pollices. The cranial elements are reduced in ossification; a large frontoparietal fontanelle is present, and the quadratojugal is much reduced and not in contact with the maxillary. Prevomerine teeth are present. The tadpoles have xiphicercal tails and a terminal mouth lacking teeth and labial papillae. The mating call consists of a primary note followed by a series of secondary notes. The haploid number of chromosomes is 15 (known only in *H. microcephala* and *phlebodes*).

COMPOSITION: Four species (*H. microcephala*, *phlebodes*, *robertmertensi*, and *sartori*) occur in Middle America. South American relatives include several species (*H. elongata*, *minuta*, *nana*, and *werneri*) widely distributed east of the Andes. Fouquette (1968) indicated that the South American *H. misera* is a subspecies of *H. microcephala*. Two subspecies of *Hyla microcephala* are recognized in Middle America; the other species are monotypic. Of the five species, 2948 preserved frogs, 37 skeletons, nine lots of tadpoles, and four preserved clutches of eggs were examined from Middle America.

COMMENTS: The members of the *Hyla microcephala* group exhibit few differences in size or proportions; minor differences exist in the structure of the hands and feet (figs. 80 and 81). The known tadpoles can be distinguished only by their coloration (fig. 82), for in size and shape they show few differences; all have greatly reduced, terminal mouths (fig. 83). The coloration and mating calls provide the easiest means of identification of the species (pls. 28, 29, and 49).

The mating calls are an insect-like series of notes, "creek-cek-cek-cek," composed of a primary note followed by a series of shorter secondary notes. The primary note of *Hyla microcephala* is unpaired, and the secondary notes are paired, whereas the opposite is true of *robertmertensi*. All notes are unpaired in *phlebodes* and *sartori*; also, the dominant frequencies are much lower in these species than in *robertmertensi* and *microcephala* (table 22). Duellman and Fouquette (1968) analyzed the mating calls of the species in this group and, among other things, showed that the only sympatric species (*microcephala* and *phlebodes*) had the most divergent calls.

Osteologically, this group of species is characterized by a minimal amount of cranial ossification. Despite the little ossification, certain cranial differences are apparent among the species. Differences in the amount of ossification of the frontoparietals and the consequent shape and size of the frontoparietal fontanelle result in *H. microcephala* having minimally ossified frontoparietals with a large fontanelle, whereas the ossification is more extensive anteriorly in the other species, thereby producing a fontanelle that is widest posteriorly in *phlebodes* and *robertmertensi* and one that is of nearly uniform width throughout its length in *sartori* (fig. 84). In *H. microcephala* the nasals are long, slender, and arcuate in dorsal view. The nasals are broader in *sartori*, and they are wider anteriorly than posteriorly in *phlebodes* and *robertmertensi*. The sphenethmoid is extremely short in *H. microcephala* and moderately short in the other species. The sphenethmoid is ossified anteriorly between the nasals in *sartori*. The distal end of the columella is expanded in *H. microcephala*, slightly expanded in some *rob-*

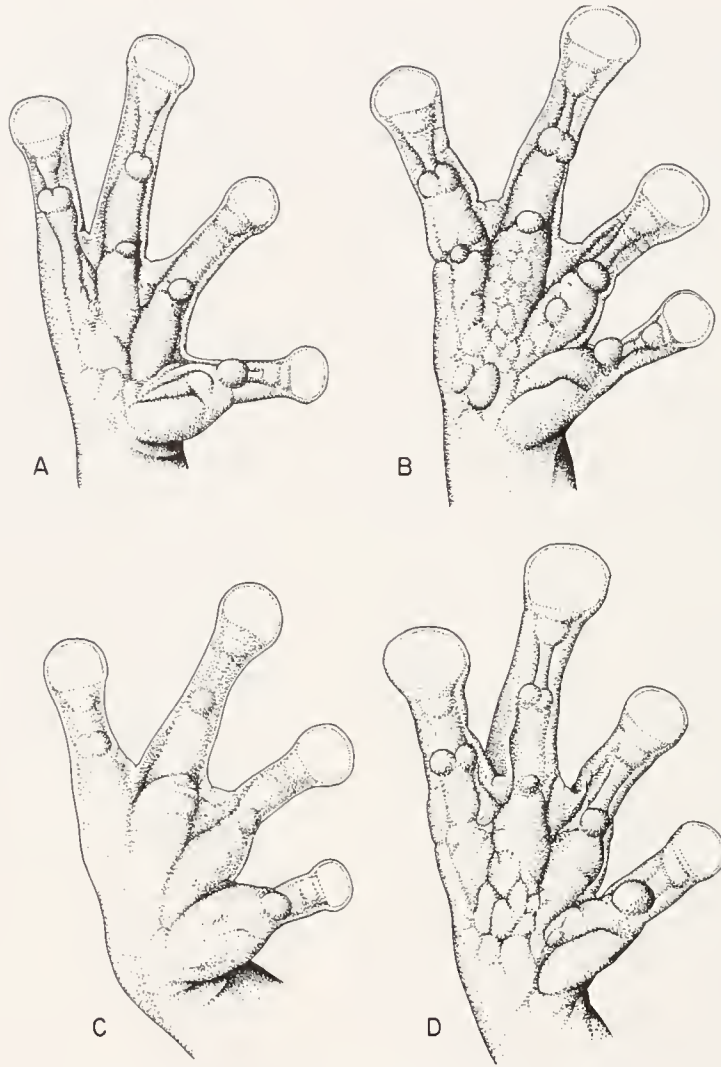


FIG. 80. Hands of the species in the *Hyla microcephala* group.
 A. *H. microcephala*, K.U. No. 101606. B. *H. robertmertensi*, K.U.
 No. 57618. C. *H. phlebodes*, K.U. No. 77270. D. *H. sartori*, K.U.
 No. 67855. $\times 8$.

ertmertensi, and not expanded in the other species. The osteological similarities are strongly suggestive of close relationships among the species in the *Hyla microcephala* group. However, the trivial differences among the species provide little evidence for determining phylogenetic lineages.

Duellman and Fouquette (1968) suggested that the *Hyla microcephala* group was first represented in Middle America by a *microcephala*-like ancestral stock which emigrated

from South America. Their phylogenetic suppositions include an early divergence into a *phlebodes*-like frog on the Caribbean lowlands of Central America and a *microcephala*-like frog on the Pacific lowlands; the former gave rise to *phlebodes* and *sartori*, and the latter evolved into *microcephala* and *robertmertensi*. No new evidence has come to light that disproves this hypothesis.

The *Hyla microcephala* group occurs at low elevations from Jalisco and Veraacruz,

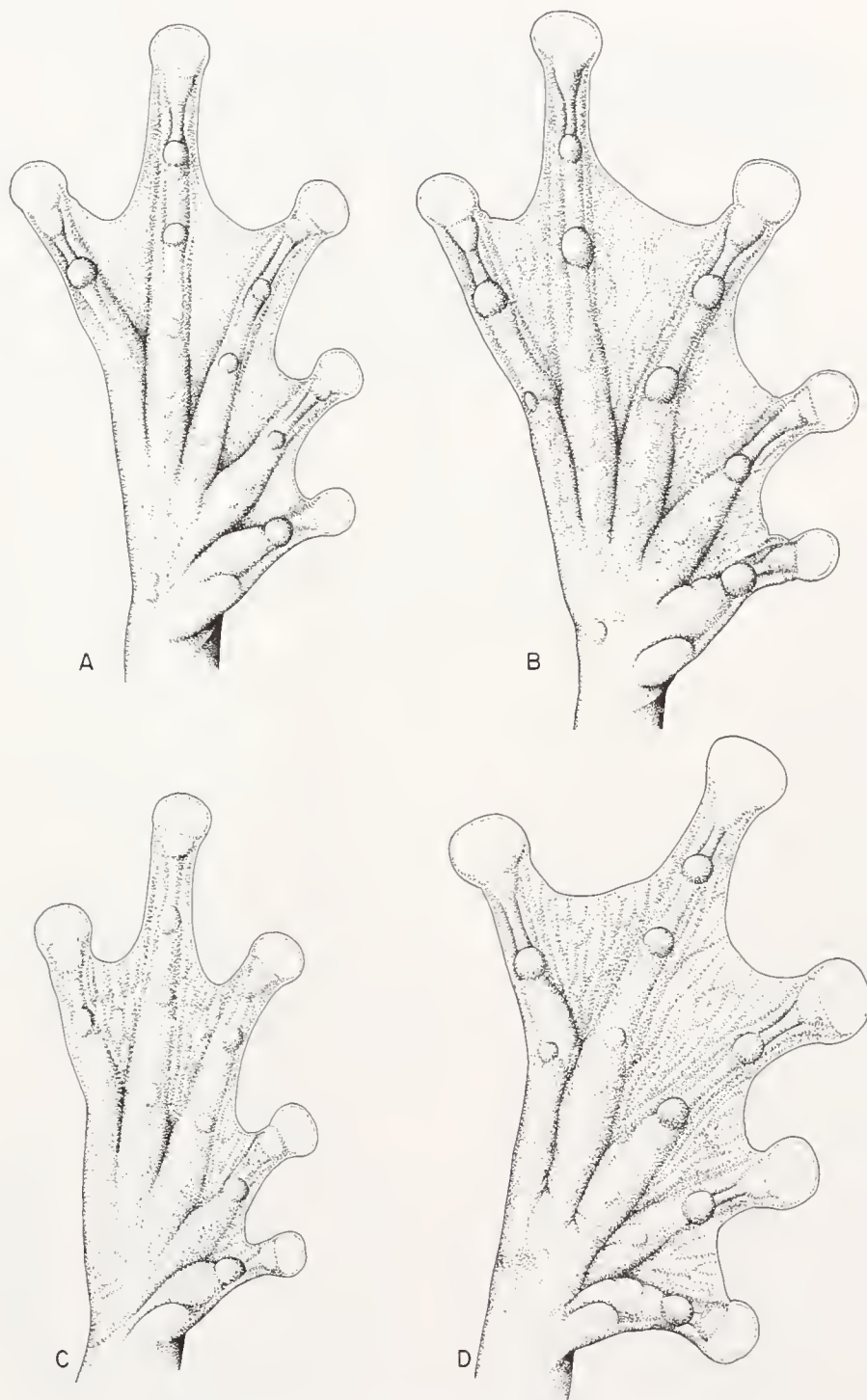


FIG. 81. Feet of the species in the *Hyla microcephala* group. A. *H. microcephala*, K.U. No. 101606. B. *H. robertmertensi*, K.U. No. 57618. C. *H. phlebodes*, K.U. No. 77270. D. *H. sartori*, K.U. No. 67855. $\times 8$.

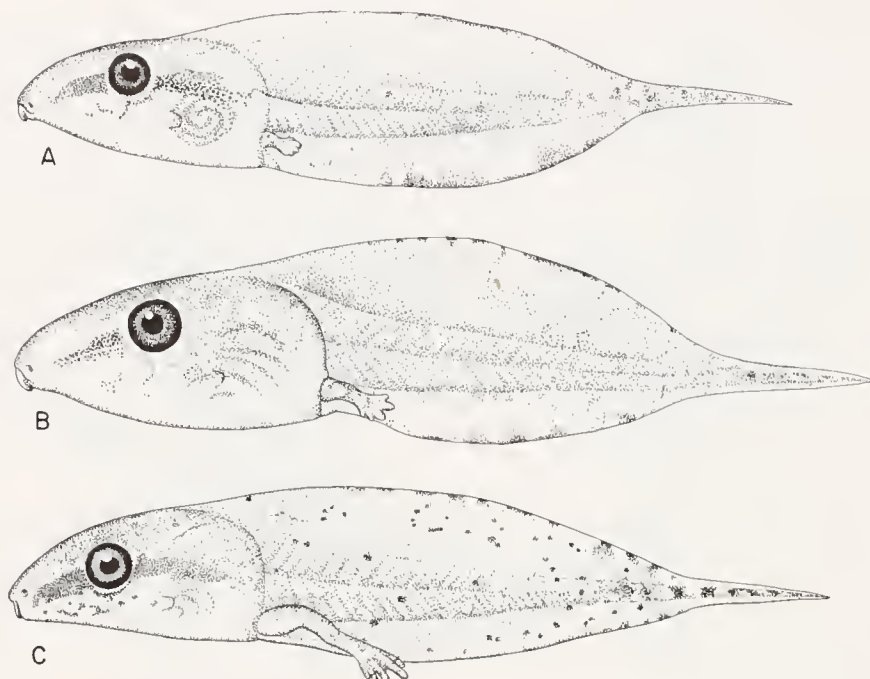


FIG. 82. Tadpoles of the *Hyla microcephala* group. A. *H. microcephala microcephala*, K.U. No. 104097. B. *H. microcephala underwoodi*, K.U. No. 106935. C. *H. phlebodes*, K.U. No. 104099. $\times 4$.

México, southeastward into South America. Members of this group are among the most common and conspicuous (by their voices) frogs in the lowlands of Middle America.

Hyla microcephala Cope

Hyla microcephala Cope, 1886, p. 281.

DIAGNOSIS: This small species is distinguished from other Middle American *Hyla* with uniformly yellow thighs by having a narrow lateral brown stripe extending to the sacral region or to the groin and bordered above by a narrow white line. The dorsum is marked by a pair of discreet longitudinal dark lines, interconnecting dark lines, or variously arranged dashes. The head is narrow, and the axillary membrane is not well developed. See the diagnoses and descriptions of the subspecies for further characteristics and comparisons.

CONTENT: Three subspecies are recognized: *Hyla m. microcephala* Cope inhabits the Pacific lowlands of southeastern Costa Rica eastward to Colombia, *H. m. misera* occurs in northern South America and the Ama-

zon Basin, and *H. m. underwoodi* Boulenger ranges from northwestern Costa Rica to México.

Although minor differences exist in some measurements and proportions and in certain parameters of the mating calls, the color pattern provides the major, and only diagnostic, differences between the subspecies. The eastern subspecies (*H. m. microcephala*) characteristically has a dorsal pattern of two continuous dark lines and no interorbital dark

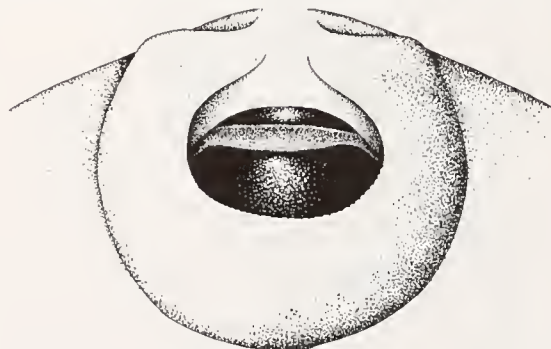


FIG. 83. Mouth of a tadpole of *Hyla microcephala microcephala*, K.U. No. 104097. $\times 48$.

TABLE 22
Characteristics of the Mating Calls, with Means in Parentheses,
of Frogs in the *Hyla microcephala* Group.

Species	N	Duration of Primary Note (seconds)	Repetition Rate of Secondaries (notes per minnte)	Fundamental Frequency (cps)	Dominant Frequency (cps)
<i>H. m. microcephala</i>	44	0.11-0.16 (0.13)	192-353 (268)	184-244 (205)	5150-5962 (5637)
<i>H. m. underwoodi</i>	47	0.05-0.15 (0.11)	197-384 (268)	192-275 (220)	5177-6200 (5772)
<i>H. robertmertensi</i>	25	0.07-0.11 (0.09)	368-570 (418)	140-178 (162)	5150-5785 (5388)
<i>H. phlebodes</i>	34	0.07-0.16 (0.11)	210-350 (284)	125-158 (148)	3220-4067 (3578)
<i>H. sartori</i>	10	0.07-0.09 (0.08)	396-477 (434)	116-135 (126)	2950-3600 (3217)

mark, whereas the northwestern subspecies (*H. m. underwoodi*) has a variegated dorsal pattern and usually has a dark interorbital mark. Also, the shanks in *H. m. microcephala* are marked with flecks or a longitudinal line, never the narrow transverse bands usually found in *H. m. underwoodi*.

DISTRIBUTION: *Hyla microcephala* occurs in the foothills and at low elevations on the Atlantic lowlands from southern Veracruz and northern Oaxaca, México, southeastward to north-central Nicaragua and thence southeastward on the Pacific lowlands to eastern Panamá (fig. 85). The species occurs in the Magdalena and Cauca valleys (Caribbean drainage) of Colombia, in northern South America and discontinuously in the Amazon Basin.

Hyla microcephala microcephala Cope

Hyla microcephala Cope, 1886, p. 281 [syntypes, U.S.N.M. No. 13473 (two specimens, now lost) from Chiriquí, Panamá; J. A. McNeil collector]. Günther, 1901 (1885-1902), p. 265.

Hyla microcephala microcephala: Smith, 1951, p. 185 [first usage of trinomial]. Duellman and Fouquette, 1968, p. 526.

DIAGNOSIS: *Hyla m. microcephala* can be distinguished from other small Middle American *Hyla* with uniformly yellow thighs by the presence of a narrow dark brown lateral stripe extending from the nostril along the canthus and the upper edge of the tympanum to the groin, bordered above by a narrow white line, yellowish tan dorsum with a pair of longitudinal dark brown lines extending to the

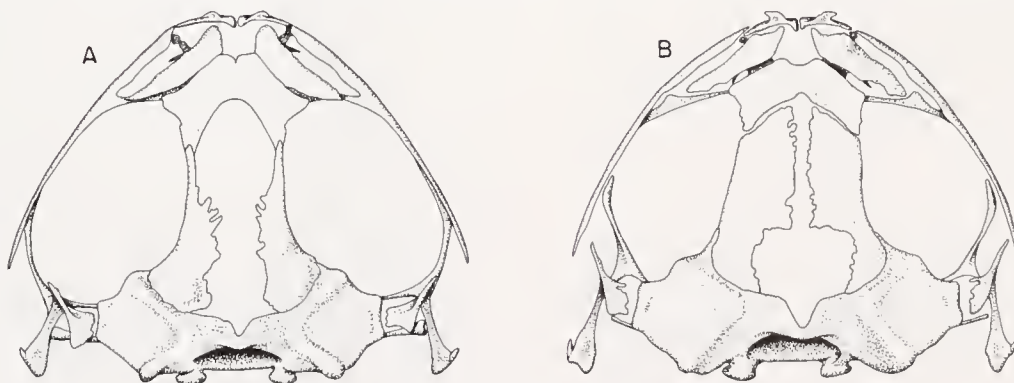


FIG. 84. Dorsal views of the skulls of two species of the *Hyla microcephala* group. A. *H. microcephala*, K.U. No. 68293. B. *H. phlebodes*, K.U. No. 68303. $\times 8$.

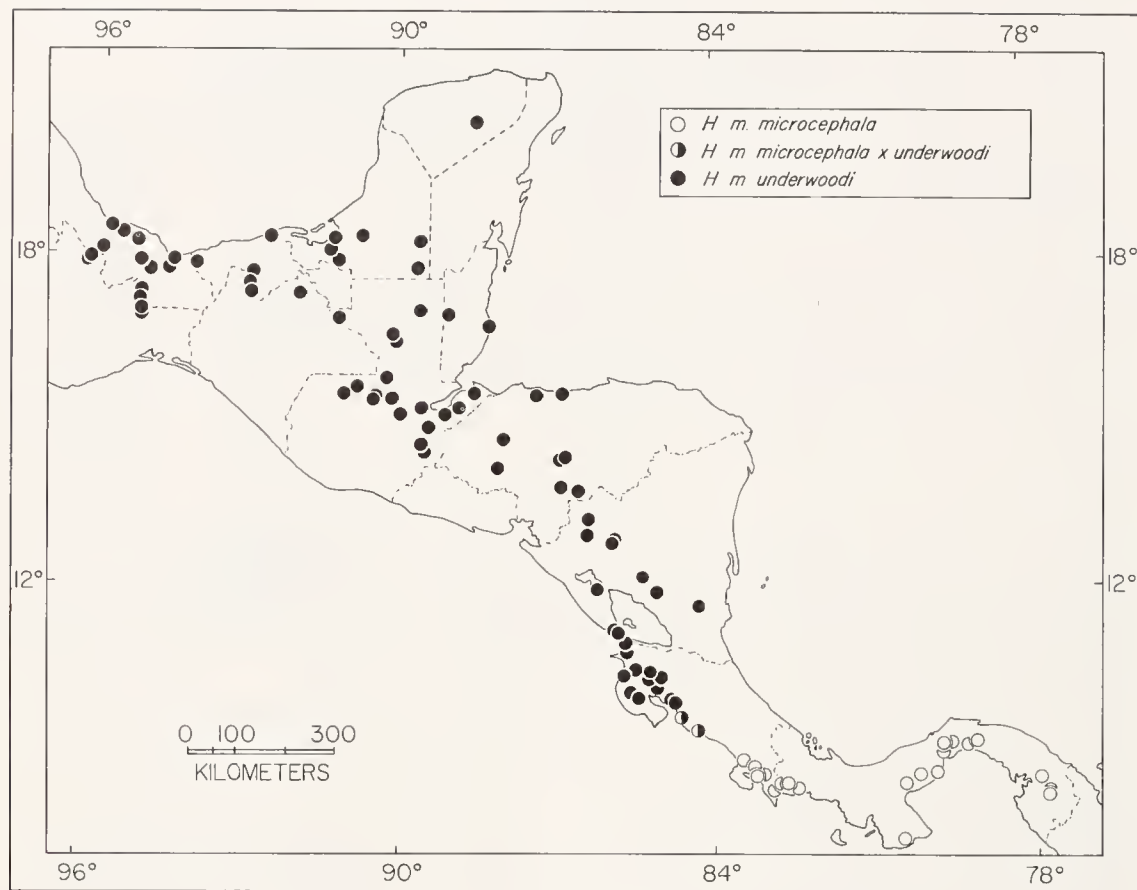


FIG. 85. Distribution of the subspecies of *Hyla microcephala*.

vent, shanks with dark flecks or longitudinal line, and by the absence of a dark interorbital mark. *Hyla m. underwoodi* differs by having irregular marks or interconnected lines on the dorsum and usually by having a dark interorbital mark and dark transverse bars on the shanks. The pattern of *Hyla robertmertensi* resembles that of *H. microcephala*, but the former has a much broader lateral brown stripe which includes the loreal region and the entire tympanum.

DESCRIPTION: This is a small slender frog; males attain a maximum snout-vent length of 24.5 mm. (mean, 25 specimens from Golfito, Costa Rica, 22.4 mm.), and females reach 30.9 (mean, nine specimens, 27.9 mm.). In a sample of 25 males from Golfito, Puntarenas Province, Costa Rica, the ratio of tibia length to snout-vent length is 0.491 to 0.544 (mean, 0.516); the ratio of foot length to snout-vent

length is 0.418 to 0.480 (mean, 0.451); the ratio of head length to snout-vent length is 0.302 to 0.355 (mean, 0.331); the ratio of head width to snout-vent length is 0.290 to 0.327 (mean, 0.308), and the ratio of the diameter of the tympanum to that of the eye is 0.400 to 0.578 (mean, 0.484). Specimens from the eastern part of the range have proportionately shorter heads; in a sample of 25 males from 8-14 kilometers north of Miraflores Locks, Canal Zone, the ratio of head length to snout-vent length is 0.285 to 0.328 (mean, 0.310).

The head is no wider than the body, and the top of the head is flat or slightly convex. In dorsal profile the snout is acutely rounded; in lateral profile the snout is truncate, but rounded above. The snout is short; the nostrils are slightly protuberant and situated about two-thirds the distance from the eyes

to the tip of the snout. The canthus is rounded and indistinct; the loreal region is barely concave, and the lips are thin and barely flared. A thin dermal fold extends posteriorly from the posterior corner of the eye to a point above the insertion of the arm; the fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is posterior and slightly ventral to the midline of the eye and separated from the eye by a distance equal to about two-thirds the diameter of the tympanum.

The arm is short and moderately robust; an abbreviated axillary membrane is present. Dermal folds along the outer edge of the forearm and across the wrist are absent. The fingers are short and broad and have large discs; the diameter of the disc on the third finger is about three-fourths the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercles on the third and fourth fingers are bifid in about 60 per cent of the specimens. The supernumerary tubercles are large, conical, and in a single row on the proximal segments of each finger. The prepollex is moderately enlarged; breeding males lack a horny nuptial excrescence. The fingers are about one-third webbed (fig. 80A). The webbing is barely evident between the first two fingers but connects the middle of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third finger. The web extends between the bases of the penultimate phalanges of the third and fourth fingers. The hind limbs are moderately short and heavy; the adpressed heels overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A weak tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, and elongate. The toes are moderately long and slender; the discs are slightly smaller than those on the fingers. The subarticular tubercles are large and round; the supernumerary tubercles are small, conical, and in a single row on the proximal segment of each toe. The toes are about three-fourths webbed (fig. 81A). The web extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate pha-

lanx of the second toe and from the base of the disc on the second toe to the base of the penultimate phalanx of the third; from the base of the disc of the third toe the web continues to the base of the penultimate phalanx of the fourth toe and on to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the level of the upper edges of the thighs. The anal sheath is short and broad. The skin is smooth, except on the belly and ventral surfaces of the thighs where it is granular. The tongue is ovoid, not or barely notched anteriorly and posteriorly, and free posteriorly for about one-fourth of its length. There are usually two to four (mean, 3.2) prevomerine teeth on small rounded processes between the large, round choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla microcephala microcephala* is yellowish tan with two brown longitudinal stripes on the back and a brown longitudinal stripe on the flank, bordered above by a narrow white line (pl. 49, fig. 1). By day, most individuals are tan or pale reddish brown dorsally with dark brown longitudinal lines and brown flecks on the back. The dorsolateral stripe, which begins on the snout and extends to the groin, is creamy tan or yellow by day. The flanks are tan or pale reddish brown. The axilla, base of arm, groin and thighs are yellow. The shanks and feet are tan with brown flecks or a faint longitudinal brown line on the shank. The belly is white; in breeding males the vocal sac is pale yellow. The iris is bronze with a brown tint anterior and posterior to the pupil. In preservative, the venter is white; the dorsum usually is creamy tan with faint brown lines. The thighs usually are pigmentless.

Little geographic variation in color pattern has been observed. Of 103 specimens from the Canal Zone, all lack an interorbital bar, and all have a dark longitudinal line on the dorsal surface of the shank. The longitudinal lines on the dorsum are continuous to the anal region in 95 specimens and fragmented in two specimens. In two others, the lines converge and fuse in the scapular region,

and in four specimens, additional fragmented lines are present dorsolaterally. The pattern is constant in all specimens from Puntarenas Province, Costa Rica, except that in about 10 per cent of the specimens the longitudinal line on the shank is replaced by brown flecks.

TADPOLES: A typical tadpole in developmental stage 34 from Chepo, Panamá, has a total length of 20.5 mm. and a body length of 8.2 mm. The body is slightly wider than deep. The snout is pointed. The nostrils are large, situated dorsally much closer to the snout than to the eyes, and are directed anteriorly. The eyes are moderately small, situated dorsolaterally, and directed laterally. The spiracle is sinistral and lies just posteroventral to the eye; the anal tube is dextral. The caudal musculature of the xiphicercal tail is moderately deep, becoming slender posteriorly and extending beyond the caudal fin. The fins are deepest at about one-third the distance from the body to the tip of the tail. The dorsal fin is deeper than the deepest part of the caudal musculature and extends onto the body. The ventral fin is slightly shallower than the caudal musculature. The small, terminal mouth lacks teeth and fringing papillae but has finely serrate beaks (fig. 83).

The top of the head and body are yellowish tan. A dark brown stripe extends from the snout through the eye to the posterior edge of the body, where the stripe narrows to a thin line midlaterally on the proximal one-fourth of the tail. The belly is white; the anterior half of the tail lacks pigment, whereas the posterior half is deep orange. The iris is pale bronze. In preserved specimens, the top of the head is pale brown, and the venter is white. The tail is creamy tan with fine black flecks, most numerous posteriorly. The posterior two-thirds of the caudal fins are edged with black (fig. 82).

MATING CALL: The call of *Hyla m. microcephala* is an insect-like "creeek-eeek-eeek-eeek." Often, especially at the beginning of a series of call groups, only the unpaired primary note is given; at other times the primary note is followed by zero to 18 (usually about four) shorter, paired secondary notes. The repetition rate of the secondaries is 192 to 353 (mean, 268) notes per minute. The duration

of the primary note is 0.11 to 0.16 (mean, 0.13) of a second, and that of the secondary notes is 0.05 to 0.14 (mean, 0.10) of a second. The primary notes are characterized by a pulse rate of 150 to 210 (mean, 183) pulses per second. Each primary note has 19 to 22 (mean, 20.5) pulses, and secondary notes have five to seven (mean, 5.8) pulses. The fundamental frequency of normal primary notes is between 184 and 244 (mean, 205) cycles per second, and the dominant frequency varies from 5150 to 5962 (mean, 5637) cycles per second (pl. 28, fig. 1). Sometimes given individuals emit exceptionally high primary notes. Fouquette (1960b) analyzed the high primary notes emitted by frogs from the Canal Zone and determined that the fundamental frequency varied from 315 to 419 (mean, 385.1) cycles per second and that the dominant frequency varied from 5300 to 5800 (mean, 5570) cycles per second.

NATURAL HISTORY: *Hyla microcephala microcephala* apparently is not an inhabitant of primary forest, but instead occurs in disturbed areas, such as cut-over forests, second growth, and pastureland. It does not occur on the *Curatella*-savannas on the Pacific lowlands of Panamá. In the Canal Zone, this small frog breeds throughout the rainy season, which extends from May through January; in the wetter coastal lowlands of eastern Puntarenas Province, Costa Rica, *H. microcephala* apparently breeds throughout the year. Breeding sites usually are shallow ditches, marshes, or temporary ponds. Calling males usually perch on grasses or reeds in, or at the edge of, the water. The eggs are deposited in small masses that float near the surface of the water and usually are attached to emergent vegetation.

REMARKS: Rivero (1961) and Duellman and Fouquette (1968) noted that *Hyla microcephala* may be conspecific with *Hyla misera* Werner, a species that is widely distributed east of the Andes in South America. The latter authors were reluctant to place the two taxa in the same species until data on the coloration in life, mating calls, and life history are available for *Hyla misera* and compared with those of *H. microcephala*. Fouquette (1968) considered *misera* as a subspecies of *microcephala*; this assignment was made principally on call data.

Duellman and Fouquette (1968) tentatively placed *Hyla cherrei* Cope in the synonymy of *H. m. microcephala*. The type specimen apparently is lost, so the only extant information regarding this taxon is that provided by Cope (1894) in the type description. A reconsideration of the status of the name *Hyla cherrei* and an attempt to treat all such "unknown species" uniformly results in the placement of *Hyla cherrei* Cope in the Nomina Dubita section of the present paper.

Evidence for intergradation between *H. m. microcephala* and *H. m. underwoodi* is provided by four specimens [U.S.C. Nos. 818 (2), 6081-6082] from 6.1 kilometers northeast of the mouth of the Río Tarcoles, and nine specimens [U.S.C. Nos. 8254 (2), 8255, 8256 (4), 8258 (2)] from Parrita, both in Puntarenas Province, Costa Rica. In these specimens the dorsal pattern varies from nearly complete longitudinal lines to broken lines, fused into an X-shaped scapular mark or not. Some specimens have longitudinal lines on the shanks, whereas others have faint transverse markings.

ETYMOLOGY: The specific name *microcephala* is derived from the Greek *mikros*, meaning small, and the Greek *kephale*, meaning head, and is in reference to the characteristic small, narrow head of the species.

DISTRIBUTION: *Hyla microcephala microcephala* inhabits coastal lowlands from the area of the Golfo Dulce (apparently absent in the Osa Peninsula) in southeastern Costa Rica eastward in Panamá, including the Azuero Peninsula, to northern Colombia and thence southward in the valleys of the Río Cauca and Río Magdalena in Colombia (fig. 85). Except for the central part of the Canal Zone, the subspecies is unknown from the Caribbean drainage in Central America, but in Colombia the subspecies occurs only in the Caribbean drainage. In Central America this frog occurs mostly on the coastal lowlands; the highest recorded elevation is 560 meters at El Valle, Coclé Province, Panamá.

See Appendix 1 for the locality records of the 477 specimens examined.

Hyla microcephala underwoodi Boulenger

Hyla microcephala Boulenger, 1898b, p. 481 [syn-types, B.M.N.H. Nos. 1947.2.23.28 and 29 from Bebe-

dero, Guanacaste Province, Costa Rica; C. F. Underwood collector (not *Hyla microcephala* Cope, 1886, p. 281, from Chiriquí Province, Panamá)].

Hyla underwoodi Boulenger, 1899, p. 277 [substitute name for *Hyla microcephala* Boulenger, 1898b (preoccupied by *Hyla microcephala* Cope, 1886, p. 281)]. Günther, 1901 (1885-1902), p. 278, Smith and Taylor, 1948, p. 85. Taylor, 1952c, p. 891.

Hyla phlebodes: Kellogg, 1932, p. 172 [not *Hyla phlebodes* Stejneger, 1906, p. 817 from San Carlos, Costa Rica].

Hyla microcephala martini Smith, 1951, p. 187 [holotype, U.I.M.N.H. No. 20965 from Encarnación, Campeche, México; Hobart M. Smith collector]. Stuart, 1963, p. 36.

Hyla microcephala underwoodi: Smith, 1951, p. 187 [placed *Hyla underwoodi* Boulenger, 1899, as a subspecies of *Hyla microcephala* Cope, 1886]. Duellman and Fouquette, 1968, p. 529.

DIAGNOSIS: *Hyla microcephala underwoodi* differs from other small Middle American *Hyla* with uniformly yellow thighs by having a narrow lateral dark brown stripe extending to the sacral region or groin, bordered above by a narrow white line, and a bold dorsal pattern consisting of variously arranged dark lines or dashes, not in the form of a pair of longitudinal lines. An interorbital dark mark usually is present, and the shanks usually have dark transverse marks. *Hyla phlebodes* differs by having a short lateral dark stripe, if present at all, and lacking a dorso-lateral white line; furthermore, the dorsal markings are much weaker than in *H. m. underwoodi*. *Hyla m. microcephala* differs by having a pair of longitudinal dark lines on the dorsum extending to the vent and the shanks with a dark longitudinal line or flecks, and by lacking a dark interorbital mark.

DESCRIPTION: Males of this small frog attain a maximum snout-vent length of 25.9 mm. (mean, 25 specimens from Alvarado, Veracruz, México, 24.1 mm.), and females reach 30.6 mm. (mean, six specimens, 29.3 mm.). In a sample of 25 males from Alvarado, Veracruz, México, the ratio of the tibia length to snout-vent length is 0.496 to 0.544 (mean, 0.511); the ratio of foot length to snout-vent length is 0.407 to 0.475 (mean, 0.426); the ratio of head length to snout-vent length is 0.299 to 0.338 (mean, 0.314); the ratio of head width to snout-vent length is 0.291 to 0.329 (mean, 0.305), and the ratio of the diameter of the tympanum to that of the eye is 0.407

to 0.538 (mean, 0.466). Although minor differences are apparent in certain proportions in five samples from throughout the range (Duellman and Fouquette, 1968, table 1), the only noticeable variant is the slightly larger tympanum in specimens from Hacienda La Cumplida, Nicaragua. In 25 males from there, the ratio of the diameter of the tympanum to that of the eye is 0.423 to 0.600 (mean, 0.493).

Structurally *Hyla microcephala underwoodi* is like the nominate subspecies; the reader is referred to the account of *Hyla microcephala microcephala* for a detailed description.

The general coloration of *Hyla microcephala underwoodi* at night consists of a pale yellow dorsum with brown or tan markings or flecks. By day the dorsum is yellowish tan or pale brown with dark brown or reddish brown markings; the thighs are uniform yellow (pl. 49, fig. 2). The venter is white, and the vocal sac in breeding males is yellow. The iris is bronze with a brown tint anterior and posterior to the pupil. The dorsal color pattern is highly variable. The markings on the back usually consist of interconnected dark lines forming an X-shaped mark in the scapular region or a pair of longitudinal lines that are either connected by crossbars or are fragmented. In other specimens, the dorsum is marked with irregular dark flecks or dashes (fig. 86). With the exception of a few specimens from Costa Rica, most specimens have a dark brown interorbital mark and distinct

dark brown transverse bars on the limbs. The lateral brown stripe extends only to the sacral region in most specimens from the northern part of the range (México and Guatemala), whereas in many individuals from Costa Rica, the stripe extends to the groin, thereby approaching the pattern characteristic of the nominate subspecies. Duellman and Fouquette (1968) presented an analysis of variation of the color pattern in 12 samples of *Hyla microcephala underwoodi*.

TADPOLES: A typical tadpole in developmental stage 37 from 10 kilometers east of Esparta, Costa Rica, has a total length of 28.0 mm. and a body length of 9.2 mm. The structure of the body and mouth is like that of the nominate subspecies. The coloration differs from that of the nominate subspecies; in *Hyla m. underwoodi* there is no dark line on the anterior part of the tail, and the tail is more heavily pigmented than in *Hyla m. microcephala* (fig. 82).

MATING CALL: The call of *H. m. underwoodi* is like that of the nominate subspecies in being an insect-like "creek-eeek-eeek-eeek." The primary note is unpaired, and the secondaries are paired. When the primary note is not given alone, it is followed by zero to 18 (usually about four) secondary notes. The repetition rate of the secondaries is 197 to 384 (mean, 283) notes per minute. The duration of the primary note is 0.05 to 0.15 (mean, 0.11) of a second and that of the secondary notes is 0.06 to 0.11 (mean, 0.09) of a second. The primary notes have a pulse

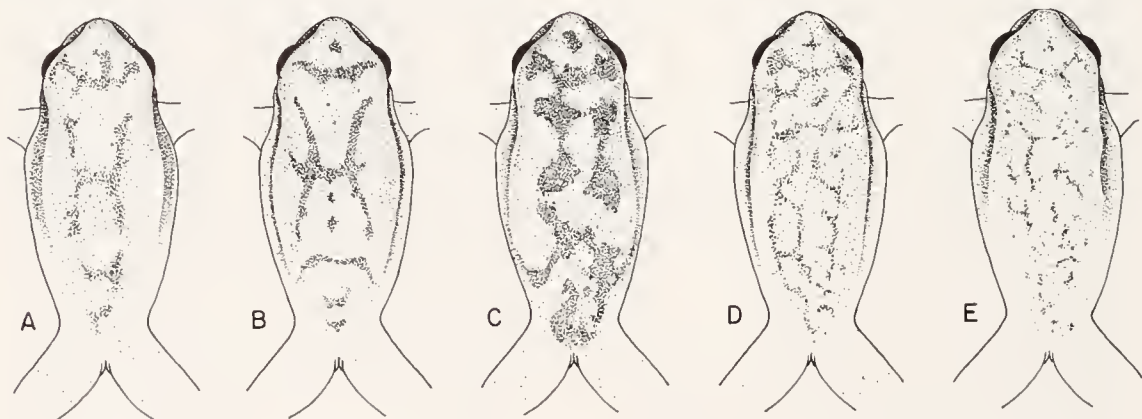


FIG. 86. Variation in dorsal color pattern in *Hyla microcephala underwoodi*. A. K.U. No. 57525. B. K.U. No. 57535. C. K.U. No. 57515. D. K.U. No. 65068. E. K.U. No. 65076.

rate of 130 to 150 (mean, 143) pulses per second. Each primary note has 19 to 22 (mean, 20.3) pulses, and secondary notes have four to six (mean, 4.8) pulses. The fundamental frequency of normal primary notes is between 192 and 275 (mean, 220) cycles per second, and the dominant frequency varies from 5177 to 6200 (mean, 5772) cycles per second (pl. 28, fig. 1). Some individuals produce high-pitched primary notes, as well as the normal notes described here.

The duration of the primary note is longest in México and shorter in the southern part of the range, although the primary notes are slightly longer in *H. m. microcephala* than in any *underwoodi*. In the latter subspecies the dominant and fundamental frequencies are lower in Costa Rica than in the more northern populations.

NATURAL HISTORY: *Hyla microcephala underwoodi* inhabits xeric and subhumid forests and savannas, where it congregates around temporary ponds in great numbers during the breeding season—usually June through September or October. Males usually call from emergent plants or grasses and sedges bordering the water. The eggs are laid in small clumps near the surface of the water and usually attached to emergent vegetation. Individuals of *H. m. underwoodi* have been found by day under the outer sheaths of banana plants next to a water-filled ditch at Tuxtepec, Oaxaca, México. At Bebedero, Costa Rica, males began calling at dusk from trees near a small marsh.

REMARKS: The confused nomenclatural history of this taxon was discussed in detail by Duellman and Fouquette (1968), so only the status of various names that have been applied are reviewed here. *Hyla underwoodi* was proposed by Boulenger (1899) as a substitute name for *Hyla microcephala* Boulenger (1898b), preoccupied by *Hyla microcephala* Cope (1886). *Hyla microcephala underwoodi*, as now recognized, has been confused with *Hyla phlebodes* Stejneger (1906).

Smith (1951) named *Hyla microcephala martini* from southern México and Guatemala and considered the northern populations to represent a subspecies distinct from the Costa Rican *Hyla microcephala underwoodi*. The

acquisition of specimens from throughout southern México and Central America negates the recognition of two taxa north of Costa Rica. Hence, *Hyla microcephala martini* Smith (1951) was placed in the synonymy of *Hyla microcephala underwoodi* Boulenger (1899) by Duellman and Fouquette (1968). The evidence for intergradation between *Hyla m. microcephala* and *H. m. underwoodi* is discussed in the account of the former subspecies.

ETYMOLOGY: The trivial name *underwoodi* is a patronym for Mr. C. F. Underwood, the collector of the type specimen in the British Museum (Natural History).

DISTRIBUTION: *Hyla microcephala underwoodi* inhabits the Atlantic slopes and lowlands from southern Vera Cruz and extreme northern Oaxaca eastward across the base of the Yucatan Peninsula to British Honduras and thence southeastward through the Caribbean lowlands and interior valleys in Honduras to central Nicaragua, where it apparently avoids the forested Caribbean lowlands and the dry Pacific lowlands of northwestern Nicaragua, but in the vicinity of Managua invades the Pacific lowlands and continues southward into northwestern Costa Rica as far as the Puntarenas Peninsula (fig. 85). In México and Guatemala the species has not been taken at elevations of more than 350 meters, whereas farther south it occurs at higher elevations—780 meters at Silencio, Costa Rica; 830 meters on Montaña de Guaimaca, Honduras; 960 meters at Finca Tepeyac, Nicaragua; and 1200 meters at Finca Venecia, Nicaragua.

The specimens from Chichén-Itzá, Yucatán, represent the only record for this species in the arid northern part of the peninsula. At least two specimens (M.C.Z. No. 2463) came from *cenotes* surrounded by evergreen vegetation. If the species is extant in the northern part of the peninsula, its distribution probably is limited to *petenes* and *cenotes*.

See Appendix 1 for the locality records of the 1389 specimens examined.

Hyla robertmertensi Taylor

Hyla robertmertensi Taylor, 1937, p. 43 [holotype, F.M.N.H. No. 100096 (formerly E.H.T.-H.M.S. No. 2270) from Tapachula, Chiapas, México; Hobart M.

Smith and Edward H. Taylor collectors]. Smith and Taylor, 1948, p. 84. Stuart, 1963, p. 36. Duellman and Fouquette, 1968, p. 534.

DIAGNOSIS: This small species can be distinguished from other Middle American *Hyla* with uniformly yellow thighs by the presence of a broad dark brown lateral stripe including the loreal region and entire tympanum and extending to the groin, bordered above by a narrow white line. The yellowish tan dorsum usually is marked by a pair of dark brown longitudinal lines or series of dashes; an inter-orbital dark mark is invariably absent. *Hyla picta* and *smithi* in northern Middle America have broader dorsolateral white lines and proportionately wider heads, and *H. m. microcephala* has a much narrower lateral dark stripe. Specimens of *H. robertmertensi* lacking dorsal markings resemble some specimens of *H. ebraccata*, in which the dorsal dark markings are absent; the latter species has a wide head, extensive axillary membrane, and a white spot below the eye, all of which serve to distinguish that species from *H. robertmertensi*.

DESCRIPTION: This is a small, slender species; males attain a maximum snout-vent length of 26.4 mm. (mean, 25 specimens from Tapanatepec, Oaxaca, 24.7 mm.), and females reach 28.1 mm. (mean, six specimens from Tapanatepec, 26.6 mm.). In a sample of 25 males from Tapanatepec the ratio of tibia length to snout-vent length is 0.441 to 0.483 (mean, 0.464); the ratio of foot length to snout-vent length is 0.391 to 0.445 (mean, 0.417); the ratio of the head length to snout-vent length is 0.261 to 0.304 (mean, 0.284); the ratio of head width to snout-vent length is 0.254 to 0.281 (mean, 0.268), and the ratio

of the diameter of the tympanum to that of the eye is 0.458 to 0.553 (mean, 0.529). Specimens from the eastern part of the range are slightly smaller; in a sample of 25 males from La Trinidad, Guatemala the maximum snout-vent length is 24.6 mm., and the mean is 23.4 mm. Furthermore, specimens from Guatemala and Chiapas differ in certain proportions from specimens from Oaxaca, which have proportionately smaller heads and larger tympani (table 23).

The head is narrower than the body; the top of the head is flat. In dorsal profile the snout is narrowed anteriorly but truncate terminally; in lateral profile the snout is truncate and slightly inclined posteroventrally. The snout is short; the nostrils are barely protuberant and situated about three-fourths the distance from the eyes to the tip of the snout. The canthus is round and indistinct; the loreal region is nearly flat, and the lips are thin and barely flared. A thin dermal fold extending from the posterior corner of the eye to a point above the insertion of the arm obscures the upper edge of the tympanum. The tympanum is faint and is situated posteroventral to the eye and separated from the eye by a distance about equal to the diameter of the tympanum.

The arm is moderately long and slender; an axillary membrane is present. Dermal folds along the outer edge of the forearm and across the wrist are absent. The fingers are short and broad; the discs are rather small, not quite as large as the tympanum. The subarticular tubercles are large and round; in most specimens the distal tubercles on the third and fourth fingers are bifid. The supernumerary

TABLE 23
Comparison of Certain Proportions, with Means in Parentheses,
of Adult Males of *Hyla robertmertensi*.

Locality	N	Tibia Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
Guatemala: La Trinidad	25	0.471-0.528 (0.499)	0.300-0.333 (0.313)	0.273-0.298 (0.285)	0.444-0.500 (0.474)
Chiapas: Acacoyagua	25	0.478-0.524 (0.504)	0.291-0.327 (0.312)	0.260-0.303 (0.281)	0.428-0.538 (0.465)
Oaxaca: Tapanatepec	25	0.441-0.483 (0.464)	0.261-0.304 (0.284)	0.254-0.281 (0.268)	0.458-0.583 (0.529)

tubercles are large, conical, and in a single row on the proximal segment of each finger. The prepollex is moderately enlarged; breeding males lack a horny nuptial excrescence. The fingers are about one-half webbed (fig. 80B). The webbing is vestigial between the first and second fingers and connects the middle of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third finger. The web extends from the middle of the antepenultimate phalanx of the third finger to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short. The adpressed heels overlap by about one-third the length of the shank, and the tibiotarsal articulation extends to the eye. A weak tarsal fold extends the length of the tarsus. The inner metatarsal tubercle is small, rounded, and elongate. The toes are moderately long and slender; the discs are smaller than those on the fingers. The subarticular tubercles are small, high, and round; the supernumerary tubercles are low and indistinct. The toes are about three-fourths webbed (fig. 81B). The web extends from the distal end of the penultimate phalanx of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, and from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the level of the upper edges of the thighs. The anal sheath is short. The skin is smooth, except on the belly and ventral surfaces of the thighs where it is granular. The tongue is small, ovoid, not or barely notched anteriorly and posteriorly, and free behind for about one-fifth of its length. There are two or three (mean, 2.7) teeth on each small prevomerine process between the small round choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla robertmertensi* is pale yellow above with a white dorsolateral line and a pale brown lateral stripe at night. By day, the dorsum is yellow-

ish tan or pale reddish tan with brown markings; the narrow dorsolateral line is creamy white, and the flanks are dark brown (pl. 49, fig. 3). Invariably the thighs are uniform yellow, the venter is white, and there is no interorbital dark mark. The dark brown on the sides of the body is continuous across the end of the snout and extends to the groin. The brown lateral stripe encompasses the entire tympanum. The narrow white line also is continuous across the snout and extends posteriorly at least to the sacral region. In most specimens, the dorsal pattern consists of flecks or dashes arranged in two parallel longitudinal rows; in some specimens, the marks are fused into parallel lines. Small brown flecks are present on the dorsal surfaces of the shanks; in some specimens, these flecks tend to form a longitudinal stripe on the shank. The iris is dull bronze with a brown tint anterior and posterior to the pupil. In breeding males the vocal sac is yellow.

In preservative, the venter is white; the dorsum is grayish tan or yellowish tan with brown or dark gray marks. The thighs usually have no pigment.

The color pattern shows little geographic variation, except in the nature of the dorsal markings. A few specimens from throughout the range lack dark markings on the dorsum between the dorsolateral white lines. The unicolor dorsum is most common in samples from southeastern Guatemala and El Salvador.

TADPOLES: The tadpoles of this species are unknown. Presumably, the tadpoles live in grassy temporary ponds and are like those of other species in the *Hyla microcephala* group in having xiphicercal tails and mouths lacking teeth and papillae.

MATING CALL: The mating call of *Hyla robertmertensi* is an insect-like "cree-eek-eek-eek," consisting of a paired primary note, usually followed by zero to 28 (mean, 3) shorter, unpaired secondary notes (pl. 28, fig. 3). The repetition rate of the secondaries is 368 to 570 (mean, 418) notes per minute. The duration of the primary notes is 0.07 to 0.11 (mean, 0.09) of a second, and that of the secondary notes is 0.03 to 0.06 (mean, 0.04) of a second. The primary notes are characterized by a pulse rate of 140 to 164 (mean, 149) pulses per second. Each primary note has

nine to 12 (mean, 10.5) pulses, and secondary notes have three or four (mean, 3.4) pulses. The fundamental frequency of primary notes is between 140 and 178 (mean, 162) cycles per second, and the dominant frequency varies from 5150 to 5785 (mean, 5388) cycles per second.

NATURAL HISTORY: *Hyla robertmertensi* inhabits the subhumid and humid lowlands and foothills. In this habitat it lives in cut-over forest and low scrubby forest. It does not seem to inhabit primary forest. The species does not occur on the xeric Plains of Tehuantepec or in the xeric scrub forest in eastern El Salvador and southern Honduras.

The dry season retreats of *Hyla robertmertensi* are not known. In the rainy season, frogs of this species congregate in large numbers at temporary ponds, where the males call from grasses, bushes, and low trees. The eggs are unknown.

REMARKS: *Hyla robertmertensi* is a distinctive species and occupies a region inhabited by only one other small pond-breeding hylid—*Hyla staufferi*. Usually the two species breed at the same season and at the same sites, although *Hyla staufferi* seems to become active when less rain has fallen than normally brings about activity in *H. robertmertensi*.

ETYMOLOGY: The specific name *robertmertensi* is a patronym for Dr. Robert Mertens of the Senckenberg Museum.

DISTRIBUTION: *Hyla robertmertensi* inhabits the Pacific lowlands and foothills, to elevations of 700 meters from extreme eastern Oaxaca (east of the Plains of Tehuantepec) southeastward to central El Salvador. The species also occurs in the Cintalapa Valley (Atlantic drainage) in southwestern Chiapas (fig. 87). The distribution of the species seems to be limited on the northwest and southeast by xeric environments. *Hyla robertmertensi* inhabits an area along the Pacific coast of Central America that has higher rainfall and more luxuriant vegetation than the regions immediately to the northwest or southeast. In addition to the localities listed in the Appendix 1, Mertens (1952b, p. 30) recorded the species from Hacienda Cuyan-Cuya, Sonsonate, El Salvador.

See Appendix 1 for the locality records of the 511 specimens examined.

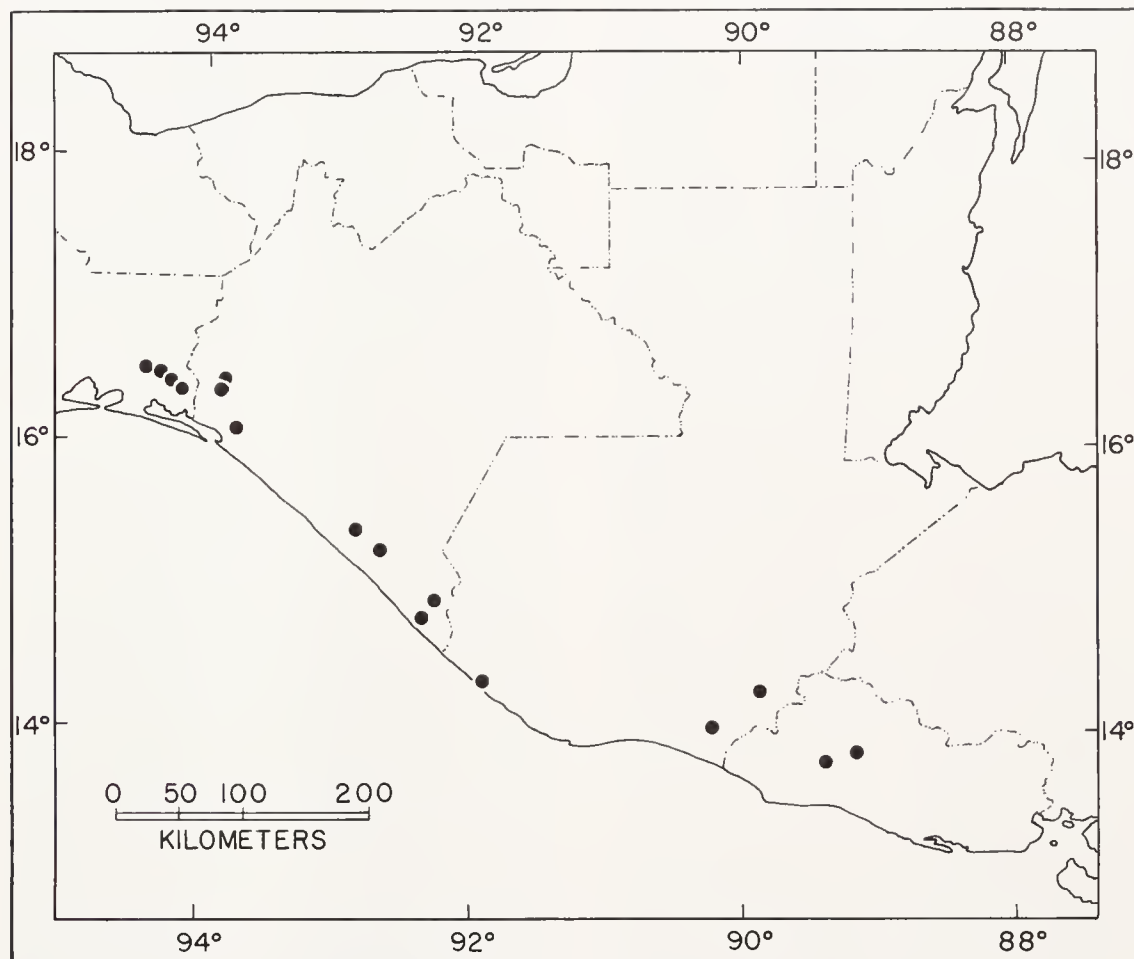
Hyla phlebodes Stejneger

Hyla phlebodes Stejneger, 1906, p. 817 [holotype, U.S.N.M. No. 2997 from "San Carlos," Alajuela Province, Costa Rica; Burgdorf and Schild collectors]. Taylor, 1952c, p. 888. Duellman and Fouquette, 1968, p. 536.

DIAGNOSIS: *Hyla phlebodes* can be distinguished from other species of Middle American hylids having uniformly yellow thighs by a yellowish tan dorsum with darker irregular dashes or interconnecting lines; if a dark brown lateral stripe is present it usually extends only to the insertion of the forearm, never posteriorly to the sacral region. *Hyla phlebodes* can be distinguished from *H. microcephala underwoodi* by having a short lateral dark stripe that is not bordered above by a narrow white line; in the latter species the lateral dark stripe extends to the sacral region or to the groin and is bordered above by a narrow white line. Furthermore, the dorsal markings of *H. microcephala underwoodi* are bolder than in *H. phlebodes*.

DESCRIPTION: This is the smallest species in the *Hyla microcephala* group. Males attain a maximum snout-vent length of 23.6 mm. (mean, 25 specimens from Turrialba, Cartago Province, Costa Rica, 22.0 mm.), and females reach 27.8 mm. (mean, seven specimens, 26.8 mm.). In a sample of 25 males from Turrialba, the ratio of tibia length to snout-vent length is 0.474 to 0.557 (mean, 0.511); the ratio of foot length to snout-vent length is 0.381 to 0.464 (mean, 0.428); the ratio of head length to snout-vent length is 0.326 to 0.359 (mean, 0.341); the ratio of head width to snout-vent length is 0.305 to 0.350 (mean, 0.329), and the ratio of the diameter of the tympanum to that of the eye is 0.357 to 0.482 (mean, 0.401). No geographic variation in size and proportions is evident among four samples from Costa Rica and Panamá.

The head is as wide as, or a little wider than, the body; the top of the head is flat. In dorsal and lateral profile, the snout is truncate. The snout is short; the nostrils are slightly protuberant and situated about two-thirds the distance from the eyes to the tip of the snout. The canthus is round and indistinct. The loreal region is barely concave, and the lips are thin and barely flared. A thin dermal fold extending from the posterior corner of the

FIG. 87. Distribution of *Hyla robertmertensi*.

eye to a point above the insertion of the arm obscures the upper edge of the tympanum, which is weakly differentiated. The tympanum is posteroventral to the eye and separated from the eye by a distance equal to half again the diameter of the tympanum.

The arm is moderately short and robust; a distinct axillary membrane is present. Dermal folds are absent on the outer edge of the forearm and across the wrist. The fingers are moderately long and slender and have large discs; the diameter of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercle on the fourth finger is bifid in about one-third of the specimens. The supernumerary tubercles are low

and indistinct. The prepollex is moderately enlarged; breeding males lack a horny nuptial excrescence. The fingers are about one-third webbed (fig. 80C). The webbing is vestigial between the first and second fingers and connects the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third and the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels overlap by about one-third the length of the shank. The tibiotarsal articulation extends to a point about midway between the eye and the nostril. A tarsal fold is absent. The inner metatarsal tubercle is low, flat, and elongate.

The toes are moderately long and slender; the discs are smaller than those on the hand. The subarticular tubercles are small and round, and the supernumerary tubercles are low and indistinct. The toes are about three-fourths webbed (fig. 81C). The web extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the level of the upper edges of the thighs. The anal sheath is extremely short. The skin is granular on the belly and proximal ventral surfaces of the thighs and smooth on other surfaces of the body. The tongue is cordiform, not or shallowly notched behind, and free posteriorly for about one-fourth its length. There are two to five (mean, 3.9) prevomerine teeth on small posteromedially slanting elevations between the small ovoid choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla phlebodes* is pale yellowish tan with weak darker brown markings on the dorsum (pl. 49, fig. 4). The flanks are pale yellow; the belly is white. The thighs are uniform yellow, and the shanks are tan with narrow brown transverse bars. The iris is creamy bronze with brown flecks and a brown tint anterior and posterior to the pupil. In breeding males, the vocal sac is yellow. In preservative, the dorsum is pale creamy gray with faint brown markings; the belly is white, and the thighs lack pigment.

A dark brown stripe extends from the nostril to the eye and thence above the tympanum to a point above the insertion of the forearm in 70 per cent of the specimens; in 17 per cent the stripe extends to midflank, and in 13 per cent the stripe is absent. A narrow, faint white line is present on the canthus in some specimens but no distinct white stripe is present above the lateral dark line posterior to the eye. An interorbital bar and transverse marks on the shanks are invariably present. The dorsal markings are variable, but in 92

percent of the specimens an X- or)(shaped mark is present in the scapular region; in other specimens, scapular markings are absent or consist of irregularly arranged short lines. A few specimens lack markings in the sacral region; most individuals have a transverse bar, chevron, or broken lines in the sacral region.

TADPOLES: Series of tadpoles are available from Puerto Viejo and Turrialba, Costa Rica. A typical tadpole in developmental stage 36 from the former locality has a total length of 21.0 mm. and a body length of 6.7 mm. The body is slightly wider than deep, and the snout is pointed. The nostrils are large and directed anteriorly near the end of the snout. The eyes are small, situated dorso-laterally, and directed laterally. The spiracle is sinistral and lies just posteroventral to the eye; the anal tube is dextral. The caudal musculature of the xiphicereal tail is moderately deep and extends well beyond the posterior edge of the caudal fin. The fins are deepest at about midlength of the tail. The dorsal fin extends onto the body and is slightly deeper than the caudal musculature; the ventral fin is slightly shallower than the musculature. The small terminal mouth lacks teeth and fringing papillae but has finely serrate beaks.

The dorsal surfaces of the head and body are reddish tan mottled with brown. A dark brown stripe extends from the snout through the eye to the posterior end of the body. The belly is white, mottled with brown and black. The caudal musculature is heavily pigmented with grayish tan, and the tip of the tail is dark gray. The caudal fins are heavily blotched with grayish tan. The iris is orange-tan peripherally and red centrally. In preservative, the dorsal surfaces of the head and body are olive-tan with brown flecks; the belly is white, flecked with brown anteriorly. The tail is creamy tan with grayish brown blotches (fig. 82C).

MATING CALL: The mating call of *Hyla phlebodes* is an insect-like "creek-eeek-eeek." Although individuals sometimes produce only primary notes, the entire mating call consists of a single, unpaired primary note followed by as many as 28 shorter, unpaired secondary notes. The note repetition rate of the secondaries is 210 to 350 (mean, 284) notes

per minute. The duration of the primary note is 0.07 to 0.16 (mean, 0.11) of a second, and that of the secondary notes is 0.04 to 0.12 (mean, 0.07) of a second. The primary notes have a pulse rate of 140 to 170 (mean, 152) pulses per second. Each primary note is composed of 13 to 15 (mean, 14.1) pulses, whereas secondary notes are made up of three to eight (mean, 5.0) pulses. The fundamental frequency of the primary notes is 125 to 158 (mean, 148) cycles per second, and the dominant frequency varies from 3220 to 4067 (mean, 3578) cycles per second (pl. 28, fig. 2).

Hyla phlebodes at Puerto Viejo, Costa Rica, produce calls with slightly lower dominant frequencies than do those from Turrialba, Costa Rica, and Panamá, whereas those at Turrialba have lower fundamental frequencies than in other samples. Calls recorded at both Costa Rican localities have slightly shorter notes than those recorded in Panamá.

NATURAL HISTORY: *Hyla phlebodes* inhabits lowland humid forests, where it breeds in shallow, grassy, temporary ponds. Since this small frog lives in areas where the rainfall is generally distributed throughout the year, males probably call throughout the year. However, large breeding congregations are most common at the early part of the rainy season. Breeding activity in *Hyla phlebodes* usually reaches a peak one or two nights after a heavy rain and not on the night of a heavy rain (Duellman and Fouquette, 1968).

Males call from grasses or sedges in, or at the edge of, ponds. The eggs are deposited in small masses that float near the surface of the water and usually are attached to emergent vegetation. The tadpoles live in shallow parts of the pond; they are most frequently found amidst submergent vegetation.

REMARKS: The literature pertaining to *Hyla phlebodes* is greatly confused, because of the misidentification of specimens and the misapplication of the name *Hyla underwoodi* Boulenger (see detailed discussion of various usages in Duellman and Fouquette, 1968). Taylor (1962c) correctly determined the application of the name *Hyla phlebodes*, although he was uncertain about the status of *Hyla underwoodi*.

Taylor (1952c) interpreted the originally

designated type locality, "San Carlos, Costa Rica," to be the "Comandancia de San Carlos at the junction of the Río Arenal and Río San Carlos"; Duellman and Fouquette (1968) suggested that the designated type locality apparently refers to the Llanuras de San Carlos, the name given to a broad lowland region in the northern part of Alajuela Province.

ETYMOLOGY: The specific name *phlebodes* is derived from the Greek *phlebos*, meaning vein, which with the Greek suffix *-odes*, meaning like, alludes to the vein-like arrangement of dark markings on the dorsum.

DISTRIBUTION: *Hyla phlebodes* ranges from southeastern Nicaragua southeastward on the Caribbean slopes and lowlands to the Canal Zone in Panamá, thence eastward in the Chucunaque Basin of eastern Panamá and on to the Pacific lowlands of Colombia (fig. 88). The species reached the Pacific slopes in the Arenal Depression in northwestern Costa Rica and in the Panamanian isthmus, where it occurs in humid forests on the Pacific slopes at El Valle and Cerro La Campana. The northern extent of the range is unknown; specimens are known from El Recreo and Isla Grande del Maíz in Nicaragua, but possibly the species occurs as far north as Bonanza. Most localities where *Hyla phlebodes* has been found are at low elevations, but the species occurs at elevations of 600 meters at Turrialba and 700 meters at Finca San Bosco in Costa Rica.

See Appendix 1 for the locality records of the 428 specimens examined.

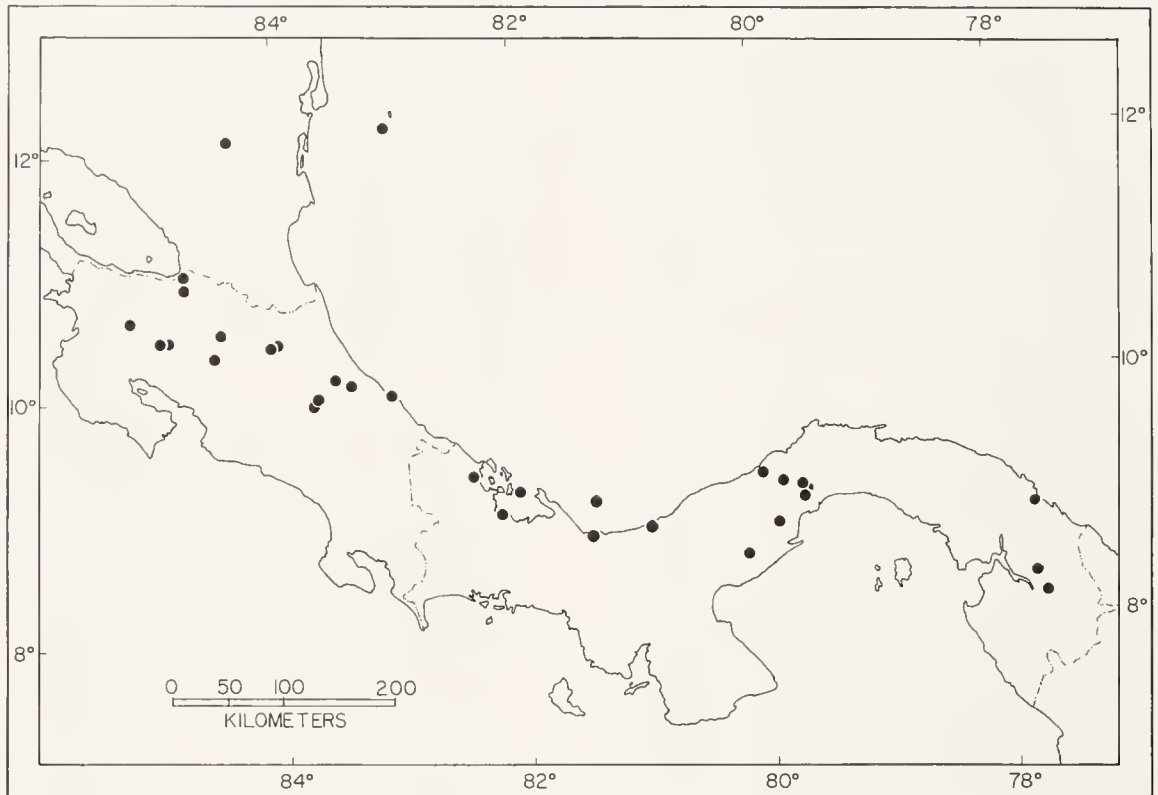
Hyla sartori Smith

Hyla underwoodi: Smith and Taylor, 1948, p. 85 [part, specimens from Guerrero].

Hyla microcephala sartori Smith, 1951, p. 186 [holotype, U.I.M.N.H. No. 20934 from 1 mile north of Organos, south of El Treinte, Guerrero, México; Hobart M. Smith and Edward H. Taylor collectors].

Hyla sartori: Savage, 1966, p. 752. Duellman and Fouquette, 1968, p. 538 [recognized *Hyla sartori* Smith, 1951, as a species distinct from *Hyla microcephala* Cope, 1886].

DIAGNOSIS: This small species is distinguished from other *Hyla* with uniformly yellow thighs by having a dark interorbital bar, broad dark brown chevrons or transverse bands on the dorsum, and two or three broad, transverse, dark brown bars on each shank,

FIG. 88. Distribution of *Hyla phlebodes*.

and by lacking a dorsolateral white stripe and extensive axillary membrane. Other small Middle American *Hyla* with uniformly yellow thighs either have no dorsal markings (*H. bromeliacea*, *dendroscarta*, and *sumichrasti*), small flecks on the dorsum (*H. melanomma*), various interconnecting or straight dark lines and at least a short white dorsolateral stripe (*H. microcephala*, *phlebodes*, and *robertmertensi*), or distinct longitudinal white stripes (*H. picta* and *smithi*). *Hyla ebraccata* has dark flanks, a white spot below the eye, no transverse bands on the shanks, an extensive axillary membrane, and an hour-glass-shaped dark mark, small dark spots, or no pattern on the dorsum.

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 26.0 mm. (mean, 25 specimens from Tierra Colorada, Guerrero, México, 24.8 mm.), and females reach 28.6 mm. In the sample of 25 males from Tierra Colorada the ratio of tibia length to snout-vent length is 0.472 to 0.514 (mean,

0.496); the ratio of foot length to snout-vent length is 0.424 to 0.478 (mean, 0.452); the ratio of head length to snout-vent length is 0.289 to 0.310 (mean, 0.300), and the ratio of the diameter of the tympanum to that of the eye is 0.423 to 0.520 (mean, 0.474). No geographic variation in size and proportions is evident.

The head is as wide as the body; the top of the head is slightly convex. In dorsal profile the snout is truncate; in lateral profile, it is bluntly rounded. The snout is short; the nostrils are slightly protuberant and situated about two-thirds of the distance from the eyes to the tip of the snout. The canthus is round and indistinct. The loreal region is concave; the lips are moderately thick and not flared. A thin dermal fold extends posteriorly from the posterior corner of the eye, covers the upper edge of the tympanum, and curves downward behind the tympanum to the place of insertion of the arm. The tympanum otherwise is distinct and is separated from the eye

by a distance equal to the diameter of the tympanum.

The arm is moderately short and robust; a distinct axillary membrane is present. Dermal folds are absent on the outer edge of the forearm and across the wrist. The fingers are short and stout. The discs are large; the diameter of the disc on the third finger equals the diameter of the tympanum. The subarticular tubercles are large and round; the distal tubercles on the third and fourth fingers are bifid in most specimens. The supernumerary tubercles are small and round; they are arranged in two rows on the proximal segment of the third finger and in one row on the other fingers. The prepollex is moderately enlarged; breeding males lack a horny nuptial excrescence. The fingers are about one-third webbed (fig. 80D). The webbing is vestigial between the first and second fingers, but extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. The tarsal fold is moderately strong and extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, and elongate. The toes are moderately long and slender; the discs are much smaller than those on the fingers. The subarticular tubercles are small and round; the supernumerary tubercles are indistinct. The toes are about three-fourths webbed (fig. 81D). The web extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. The anal sheath is short. The belly and ventral surfaces of the thighs are granular; the skin on the other surfaces is smooth. The tongue is cordiform, shallowly notched behind or not, and

free posteriorly for about one-fourth of its length. There are three or four (mean, 3.7) prevomerine teeth on elongate medially slanting elevations between the elliptical choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration at night is pale yellowish tan with broad transverse dark brown markings on the back; by day the dorsum is reddish tan with brown markings (pl. 49, fig. 5). The flanks are pale yellowish tan, and the thighs are yellow. The side of the head is brown; a narrow white line is present along the canthal ridge. A dark brown interorbital bar is invariably present. The markings on the back consist of a broad brown chevron in the scapular region and a chevron or transverse bar in the sacral region. The thighs are marked by two or three dark brown transverse bars. The belly is white; in breeding males the vocal sac is yellow. The iris is dark bronze with a brown tint anterior and posterior to the eye. By day some individuals become creamy gray with indistinct darker markings.

In preservative, the dorsum is tan or gray with brown markings; the belly is creamy white, and the thighs lack pigment.

TADPOLES: The tadpoles of *Hyla sartori* have not been found. Probably they live in shallow ponds like those inhabited by tadpoles of other species in the *Hyla microcephala* group.

MATING CALL: *Hyla sartori* has a mating call consisting of an insect-like series of notes. Although individuals sometimes emit only single notes, the complete mating call consists of an unpaired primary note followed by as many as 23 shorter, unpaired secondary notes. The note repetition rate of the secondaries is 396 to 477 (mean, 434) notes per minute. The duration of the primary note varies from 0.07 to 0.09 (mean, 0.08) of a second and of the secondaries from 0.04 to 0.07 (mean, 0.05) of a second. The primary notes have a pulse rate of 140 to 160 (mean, 149) pulses per second. Primary notes are composed of seven to 10 (mean, 8.5) pulses, whereas secondary notes are made up of three to five (mean, 3.4) pulses. The fundamental frequency of

the primary notes vary from 116 to 135 (mean, 126) cycles per second, and the dominant frequency varies from 2950 to 3600 (mean, 3217) cycles per second (pl. 29, fig. 3).

NATURAL HISTORY: This is the least known species in the *Hyla microcephala* group. After heavy rains, breeding congregations have been found at temporary ponds and at a pool in a stream. Males call from grasses, bushes, and low trees around the ponds. Because *Hyla sartori* inhabits a drier region having a relatively shorter rainy season than do other species in the *Hyla microcephala* group, the breeding season of *sartori* probably is more restricted than that of the other species.

REMARKS: Smith (1951, p. 186) named *Hyla sartori* as a subspecies of *Hyla microcephala*. Duellman and Fouquette (1968) demonstrated that on the basis of mating call and certain morphological characters *sartori* was more closely related to *phlebodes* than *microcephala*. Savage (1966, p. 752) prematurely used the combination *Hyla sartori* without providing evidence for the specific recognition.

ETYMOLOGY: The specific name *sartori* is "from the Latin *sartor*, meaning tailor; here used loosely in reference to Edward H. Taylor . . ." (Smith, 1951, p. 186).

DISTRIBUTION: *Hyla sartori* is known from mesophytic forests to elevations of about 300 meters on the Pacific slopes of southern México from southwestern Jalisco to south-central Oaxaca (fig. 89). The absence of specimens from Michoacán and Colima probably is an artifact of collecting. The species probably occurs in southwestern Nayarit. The xeric Plains of Tehuantepec apparently limit the eastward distribution of the species.

See Appendix 1 for the locality records of the 193 specimens examined.

The *Hyla leucophyllata* Group

DEFINITION: The members of this group are small species; males attain a maximum snout-vent length of about 35 mm. and females, 42 mm. The dorsum is white, yellow, or tan with or without dark brown spots or large markings. In at least one species, most of the dorsum is brown, and the ground color is reduced to a network of fine lines. The thighs are colorless in preservative but are yellow, orange, pink or red in life. The palpebral membrane is clear. The fingers are about one-half webbed, and the toes are about three-fourths webbed. Dermal folds and appendages are lacking on the limbs.

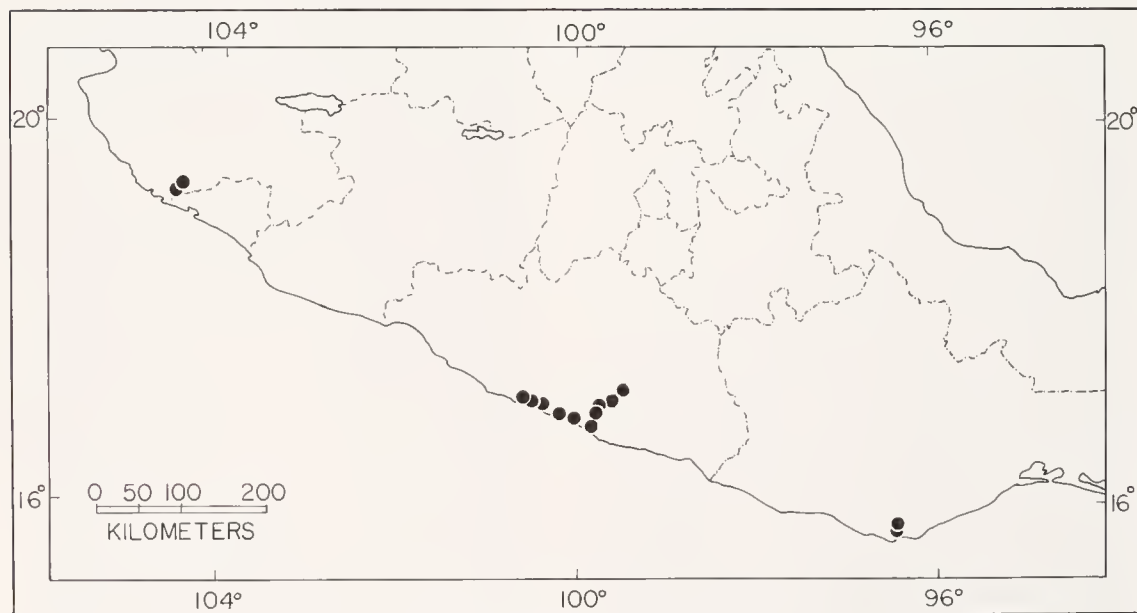


FIG. 89. Distribution of *Hyla sartori*.

The axillary membrane is extensive, and a pair of oval glandular areas are present on the chest. Males have single, median, subgular vocal sacs, but lack nuptial excrescences on the pollices. The ossification of the cranial elements is moderately reduced (fig. 90). An elongate frontoparietal fontanelle is present, and the quadratojugal is much reduced and not in contact with the maxillary. The sphenethmoid is much wider than long, and the anterior arm of the squamosal is short and extends about one-fourth the distance to the maxillary. Prevomerine teeth are present. The known tadpoles have xiphicercal tails and a terminal mouth lacking teeth and labial papillae. The mating call consists of a distinctly pulsed primary note followed or not by one or more secondary notes. In those species for which counts have been obtained, the haploid number of chromosomes is 15.

COMPOSITION: Only one species, *Hyla ebraccata*, occurs in Middle America, whereas at least 10 species are currently recognized in South America. Of the single Middle American species, 1214 preserved frogs, 33 skeletons, seven lots of tadpoles, and four preserved clutches of eggs have been examined.

COMMENTS: Obviously, Middle America is a peripheral part of the distribution of the *Hyla leucophyllata* group, which is widespread in the Amazon Basin. The greatest diversity is in the western part of the basin and on the lower slopes of the Andes, where eight nominal species are found. Too little is known about the coloration in life and of the mating

calls of these populations to determine their taxonomic relationships. Perhaps, as suggested by Duellman (1966b), some of the currently recognized species are only color variants of a single species.

The Middle American species, *Hyla ebraccata*, apparently is a post Pliocene invader into Middle America, where it occurs principally on the humid Caribbean and Gulf lowlands.

Hyla ebraccata Cope

Hyla ebraccata Cope, 1874, p. 69 [holotype, A.N.S.P. No. 2079 from Machuca, Zelaya Province, Nicaragua; John F. Bransford collector]. Brocchi, 1882, p. 44. Smith and Taylor, 1948, p. 84. Taylor, 1952c, p. 885. Stuart, 1963, p. 35. Duellman, 1966b, p. 267 [placed *Hyla weyeri* Taylor, 1954, in the synonymy of *Hyla ebraccata*].

Hyla leucophyllata: Boulenger, 1882a, p. 387 [part]. Günther, 1901 (1885-1902), p. 277. Taylor, 1942, p. 80.

Hyla weyeri Taylor, 1945b, p. 633 [holotype, K.U. No. 34850 from Esquinas Forest Preserve, Las Esquinas, between Palmar and Golfito, Puntarenas Province, Costa Rica; Mrs. Albert E. Weyer collector].

DIAGNOSIS: This is a small species characterized by a rather short, truncate snout, extensive axillary membrane, yellowish tan or yellow dorsum with or without dark brown markings, and uniformly yellow thighs. From the South American *Hyla leucophyllata*, *ebraccata* may be distinguished by the presence of an expanded white or yellow spot below the eye. The only other Middle American hylid with an extensive axillary membrane and a yellowish tan dorsum is the stream-breeding *Hyla melanomma*, which has a pointed snout, no transverse markings on the forearms and shanks, and usually a dorsal pattern consisting of small dark flecks. Of the other small Middle American hylids having an axillary membrane and uniformly yellow thighs, *Hyla microcephala microcephala*, *picta*, *robertmertensi*, and *smithi* have dorsolateral, longitudinal white stripes. *Hyla microcephala underwoodi* and *H. phlebodes* have a dorsal pattern consisting of irregular brown dashes on a tan or yellowish tan dorsum. *Hyla subocularis* has a black bordered yellow spot on the thigh. The only other Middle American hylids that are predominately yellow or yellowish tan are *Hyla bromeliacia* and *sumichrasti*; both lack an axillary membrane.

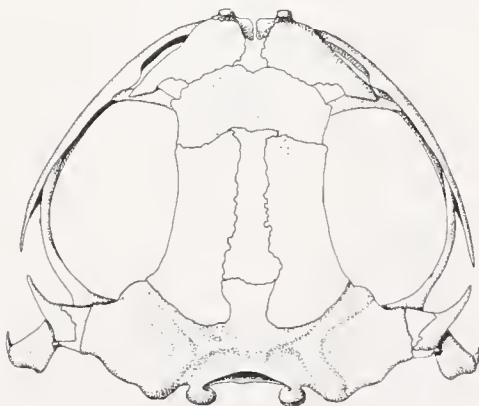


FIG. 90. Skull of *Hyla ebraccata*, K.U. No. 77686. $\times 6$.

DESCRIPTION: This is a small, rather broad-headed frog; males attain a maximum snout-vent length of 27.8 mm., and females reach 36.5 mm. In a sample of 25 males from Pacuare, Cartago Province, Costa Rica, the snout-vent length is 23.1 to 27.1 (mean, 25.1) mm.; the ratio of tibia length to snout-vent length is 0.488 to 0.566 (mean, 0.527); the ratio of foot length to snout-vent length is 0.435 to 0.472 (mean, 0.449); the ratio of head length to snout-vent length is 0.279 to 0.339 (mean, 0.311); the ratio of head width to snout-vent length is 0.301 to 0.370 (mean, 0.330), and the ratio of the diameter of the tympanum to that of the eye is 0.333 to 0.462 (mean, 0.399). Few noticeable differences exist in size and proportions from throughout the range of the species in México and Central America (table 24). The largest individuals are from the eastern part of the range in Darién Province, Panamá; specimens from El Petén, Guatemala, have the relatively shortest tibia length.

Except in gravid females, the head is wider than the body, and the top of the head is flat or slightly convex. In dorsal profile, the snout is truncate; in lateral profile, the snout is truncate and angled posteroventrally. The snout is short; the nostrils are slightly protuberant and situated about four-fifths the distance from the eyes to the tip of the snout. The canthus is rounded and indistinct; the loreal region is barely concave, and the lips are moderately thin and barely flared. A thin

dermal fold extends posteriorly from the posterior corner of the eye to a point above the insertion of the arm; the fold obscures the upper edge of the tympanum. Only the anteroventral edge of the tympanum bears a distinct rim; the rest of the tympanum is barely discernible beneath the skin. The tympanum is posterior to the eye and separated from the eye by a distance equal to the diameter of the tympanum.

The arm is moderately short and robust; the axillary membrane extends nearly to the elbow. An indistinct glandular area, oval in shape, is present in some specimens just posterior to the insertion of the arm on the belly. There is no dermal fold along the outer edge of the forearm; an indistinct transverse fold is present on the wrist. The fingers are short and broad and have large discs, the diameter of the disc on the third finger is usually slightly larger than the diameter of the tympanum. The subarticular tubercles are moderately large, round, and subconical; the distal tubercle on the fourth finger is bifid in nearly all specimens. The supernumerary tubercles are large, round, and present in a single row on the proximal segment of each digit; in some individuals additional supernumerary tubercles are present on the proximal segments of the third and fourth fingers. A large, flat, bifurcate palmar tubercle is present. The prepollex is moderately enlarged; breeding males lack a horny nuptial excrescence. The fingers

TABLE 24
Comparison of Sizes and Certain Proportions, with Means in Parentheses,
of Adult Males of *Hyla ebraccata*.

Locality	N	Snout-vent Length	Tibia Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
Guatemala:						
Toocog	25	23.9-28.3 (25.9)	0.490-0.549 (0.515)	0.283-0.344 (0.313)	0.309-0.348 (0.325)	0.344-0.464 (0.392)
Costa Rica:						
Pacuare	25	23.1-27.1 (25.1)	0.488-0.566 (0.527)	0.279-0.339 (0.311)	0.301-0.370 (0.330)	0.333-0.462 (0.399)
Costa Rica:						
Rincón de Osa	25	23.8-25.6 (24.8)	0.514-0.580 (0.548)	0.301-0.345 (0.318)	0.317-0.349 (0.311)	0.282-0.452 (0.360)
Panamá:						
Tacarcuna	25	25.8-29.3 (27.8)	0.502-0.558 (0.534)	0.288-0.328 (0.306)	0.326-0.355 (0.338)	0.352-0.484 (0.422)

are about one-half webbed (fig. 91A). The web is vestigial between the first and second fingers, but extends from the middle of the penultimate phalanx of the second finger to the base of the penultimate phalanx of the third and on to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and slender; the adpressed heels overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A thin, flap-like tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, and elliptical; the tubercle is barely visible from above. A minute outer metatarsal tubercle is present. The toes are long and slender; the discs are smaller than those on the fingers. The subarticular tubercles are moderately large, round, and sub-conical. Minute supernumerary tubercles are present on the proximal segments of all digits. The toes are about three-fourths webbed (fig. 91B). The web extends from the base of the disc of the first to the distal end of the penultimate phalanx of the second and on to the base of the penultimate phalanx of the third toe; the web continues from the base of the disc of the third toe to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the level of the upper edges of the thighs. No anal sheath, as such, is present. The skin is smooth, except on the belly and ventral surfaces of the thighs where it is granular. The tongue is narrowly elliptical, about twice as long as wide, not or barely notched posteriorly and only slightly free behind. There are usually one or two prevomerine teeth on each of the posteromedially slanting elevated processes between the small, round choanae. Of 25 males from Pacuare, Cartago Province, Costa Rica, five individuals lack prevomerine teeth, and one individual has three teeth on one side and two on the other. Most females from the same locality have three teeth on each prevomerine process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla ebraccata* is

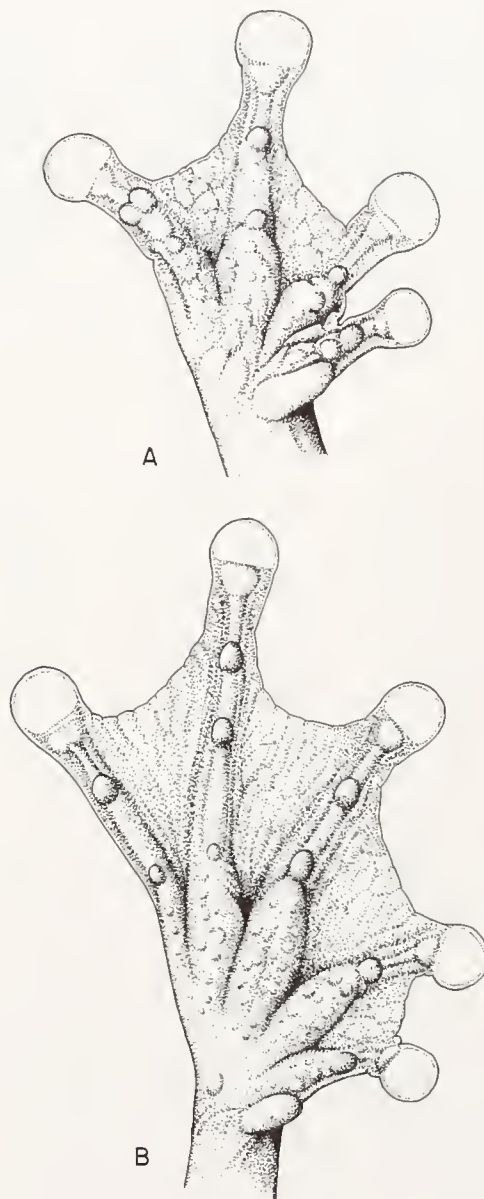


FIG. 91. Hand (A) and foot (B) of *Hyla ebraccata*, K.U. No. 77121. $\times 7$.

pale yellow or yellowish tan with dark brown dorsal markings (pl. 49, fig. 7). When active at night, the frogs usually are pale yellowish tan with the dorsal markings barely discernible. By day the contrasting dorsal coloration is apparent. The thighs in all individuals are uniformly yellow or pale orange. Most of the upper arm, the inner surface of the foot, the

hands, and the feet are pale yellow. Likewise, the flanks are pale yellow and give way ventrally to creamy white on the belly. The side of the head including the tympanum is dark brown, except for a narrow creamy white or yellow labial stripe which in most specimens is broadly expanded into a noticeable subocular spot. The dorsal yellow markings on the body, forearm, and shanks, turn white by day in some individuals. Usually, in these same individuals, the brown markings are outlined by a darker brown. The iris is reddish bronze or reddish tan with red flecks. In breeding males the vocal sac is bright yellow.

In preserved specimens, the dorsal markings are brown, and the dorsal ground color is creamy white or tan. The thighs lack pigment and the venter is creamy tan.

The dorsal dark markings in *Hyla ebracata* usually consist of an hourglass-shaped mark that extends from the eyelids to the sacral region, where in most specimens the posterolateral corners of the hourglass are confluent with the dark markings on the side. The shape of this dorsal mark is highly variable; in each population sampled throughout the range in Middle America various permutations of the pattern have been observed. In the northern part of the range, in México and Guatemala, all individuals have some form of the dark dorsal markings, except one specimen from Teapa, Tabasco, which has a uniform tan dorsum. In several individuals the hourglass is narrowed medially, and in some the anterior part of the mark is separated from the posterior part. In other individuals, the posterior part of the mark is further reduced or fragmented, so that the only apparent dorsal mark is a triangle in the occipital region (fig. 92). In Costa Rica and western Panamá, numerous individuals have the dorsal markings reduced to spots or flecks, and some individuals are uniform yellowish tan above (pl. 49, fig. 8). The highest incidence of plain (unmarked) individuals is on the Pacific lowlands of Puntarenas Province, Costa Rica, where approximately half of the specimens lack dorsal markings. Although the frogs from southern Costa Rica and western Panamá are especially variable, the "normal" pattern is prevalent in all of the populations sampled (table 25).

TADPOLES: Ten hatchlings from Puerto Viejo, Heredia Province, Costa Rica, have total lengths of 5.7 to 6.1 (mean, 5.91) mm., and 11 hatchlings from Toocog, El Petén, Guatemala, have total lengths of 4.5 to 5.0 (mean, 4.77) mm. The largest tadpole examined is an individual in developmental stage 40 having a body length of 11.0 mm. and a total length of 31.2 mm. A typical tadpole in developmental stage 36 from Puerto Viejo, Heredia Province, Costa Rica, has a total length of 29.4 mm. and a body length of 9.6 mm. The body is as wide as deep. In dorsal profile the snout is bluntly rounded; in lateral profile it is slightly pointed. The nostrils are rather small and are situated dorso-laterally at a point about equidistant between the snout and the eyes. The eyes are large and directed laterally. The spiracle is sinistral and lies just posteroventral to the eye; the anal tube is long and median. The tail is xiphocercal, and the caudal musculature is moderately deep anteriorly but slender distally. The fins are deepest at about midlength of the tail. The small, terminal mouth lacks teeth. There is no upper lip, and the lower lip is replaced by a heavy fleshy fold that bears papillae-like protuberances. The upper beak is shallow and forms a broad, uniform arch; the lower beak is massive. Both beaks bear fine serrations (fig. 93).

The dorsum is dark brown mottled with tan which tends to form a chevron-shaped mark with the apex at the mouth. Laterally, the pigment is interrupted by a broken white stripe extending from the mouth posteriorly below the eye along the body and onto the tail. The venter is white medially and mottled with gray peripherally. The caudal musculature is marked with a longitudinal gray stripe. The caudal fins are heavily pigmented with gray or black blotches. The pale areas on the caudal fin are rose-red. The iris is bronze peripherally and red centrally.

In preservative, the tadpoles are yellowish brown on the dorsal part of the body and the caudal fin. A dark brown stripe extends from the tip of the snout to the eye; a stripe or row of dark spots is evident on each side of the caudal musculature. The sides of the body are gray with brown reticulations. The venter is creamy white. The caudal fins are trans-

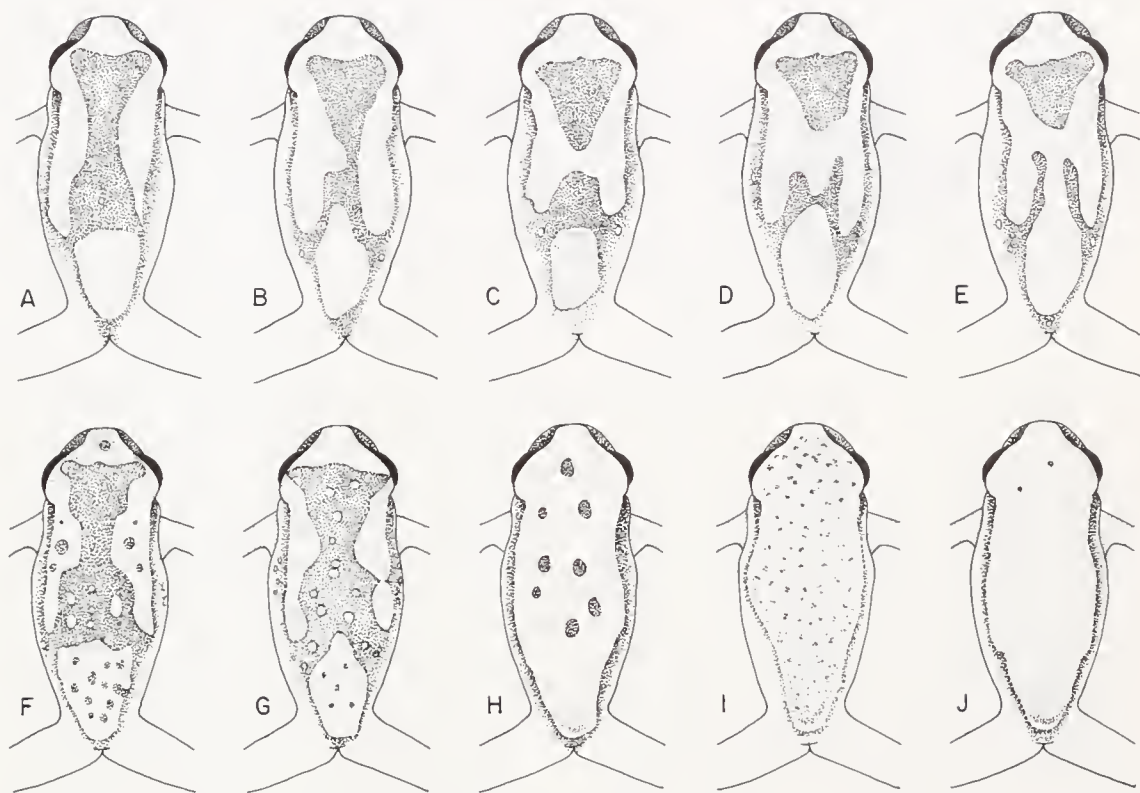


FIG. 92. Variation in the dorsal color pattern in *Hyla ebraccata*. A. K.U. No. 57292. B. K.U. No. 57295. C. K.U. No. 57277. D. K.U. No. 57287. E. K.U. No. 57291. F. K.U. No. 77050. G. K.U. No. 77052. H. K.U. No. 77044. I. K.U. No. 77077. J. K.U. No. 77073. A-E from Toocog, El Petén, Guatemala; F-J from Achiote, Colón, Panamá. $\times 3$.

TABLE 25

Geographical Distribution of Color Pattern Variants in *Hyla ebraccata*.

Locality	Hourglass	Triangle	Spotted	Plain	Total
Valle Nacional, Oaxaca, México	19	---	---	---	19
Teapa, Tabasco, México	13	2	---	1	16
Toocog, El Petén, Guatemala	47	6	---	---	53
Turrialba, Cartago, Costa Rica	87	---	---	---	87
Pacuare, Cartago, Costa Rica	48	---	---	---	48
Moravia, Cartago, Costa Rica	21	---	---	---	21
Suretka, Limón, Costa Rica	45	---	6	14	65
Tilarán, Guanacaste, Costa Rica	50	---	3	15	68
Palmar-Golfito, Puntarenas, Costa Rica	7	---	---	6	13
Rincón de Osa, Puntarenas, Costa Rica	23	---	2	4	30
Achiote, Colón, Panamá	46	---	16	15	77
Cerro La Campana, Panamá, Panamá	16	---	3	---	19
Tacarcuna-Río Mono, Darién, Panamá	63	---	---	---	63
Totals	485	8	30	55	579

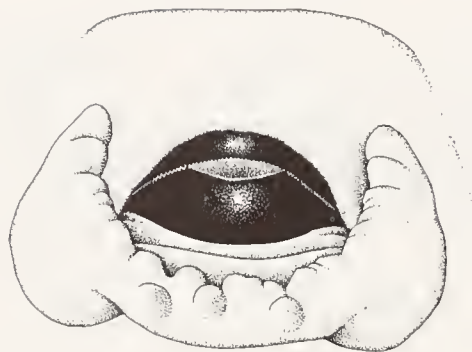


FIG. 93. Mouth of a tadpole of *Hyla ebraccata*, K.U. No. 104130. $\times 40$.

parent with dark brown blotches or vertical bars (fig. 94).

Tadpoles from Toocog, El Petén, Guatemala, were more colorfully marked in life. A black stripe was present on each side of the body and on the top of the head; a black band was present on the anterior part of the tail and another on the posterior part. The body and the anterior part of the tail were creamy yellow; a dark red vertical band was present between the black bands on the tail. Tadpoles from Tacarcuna, Darién Province, Panamá, had red on the posterior part of the caudal musculature and fins; otherwise they were marked like those from Costa Rica and Guatemala.

MATING CALL: The call of *Hyla ebraccata* is a moderately low insect-like "creek" followed, or not, by one or more secondary notes. The primary note is a single, pulsed note, whereas the secondary notes are paired. The repetition rate of the secondary notes is 210 to 429 (mean, 311.5) notes per minute. In a sample from Toocog, El Petén, Guatemala, the pulse rate is 93 to 102 (mean, 97.2) pulses per second. The duration of the primary notes in this population are 0.12 to 0.18 (mean, 0.16) of a second and that of the secondary

notes is 0.02 to 0.05 (mean, 0.03) of a second. The dominant frequency of the primary note varies from 2300 to 2650 (mean, 2504) cycles per second. Each primary note has 11 to 17 (mean, 14.2) pulses (pl. 29, fig. 1).

Some geographic variation is evident in the call of *Hyla ebraccata* (table 26). Recordings of individuals from Guatemala, the Caribbean slopes of Costa Rica, and the Pacific lowlands of Costa Rica, plus the data given for the species in the Canal Zone given by Fouquette (1960b) show that there is an increase in the duration of the primary note from north to south and an increase in the dominant frequency. A comparison of the characteristics of the calls from Guatemala with those from Costa Rica show that the latter have a slower pulse rate. In Guatemala, approximately 70 per cent of the calls were compound, that is, each call was composed of a primary plus one or more secondary notes. On the Pacific lowlands of Costa Rica, only 10 per cent of the calls are compound, whereas in the Canal Zone, Fouquette (1960b) found that 54 per cent of the calls were compound. Fouquette (1960b) described the existence of a high primary note that is emitted by some individuals from the Canal Zone. Occasional frogs were heard to emit high notes in Costa Rica and in Panamá, but high notes were not heard in Guatemala.

NATURAL HISTORY: *Hyla ebraccata* is an inhabitant of primary humid tropical forest; the species also occurs in cut-over forest and in some places in areas where most of the forest has been removed. Throughout most of its range the species lives in areas receiving rainfall throughout most of the year; the breeding season apparently is dependent upon moderately heavy to heavy rains. For example, the breeding season is closely correlated with the rainy season extending from June through September in southern México and Guatemala and is more extensive in lower

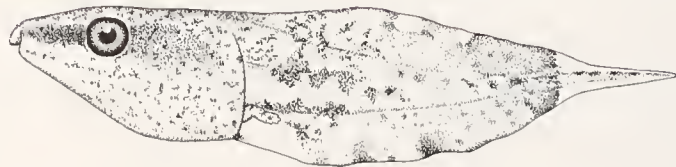


FIG. 94. Tadpole of *Hyla ebraccata*, K.U. No. 104130. $\times 3$.

TABLE 26
Geographic Variation in Mating Calls, with Means in Parentheses, of *Hyla ebraccata*.

Locality	N	Duration of Primary Note	Pulse Rate (pulses per second)	Dominant Frequency (cps)
Guatemala: El Petén	9	0.12-0.18 (0.16)	93-102 (97)	2300-2650 (2504)
Costa Rica: Caribbean	6	0.16-0.23 (0.20)	88-95 (92)	2520-2600 (2570)
Costa Rica: Pacific	9	0.16-0.24 (0.19)	90-96 (91)	2690-2940 (2790)
Panamá: Canal Zone ^a	19	0.16-0.29 (0.21)	2500-3450 (3064)

^a From Fouquette (1960b, p. 491).

Central America, for example, in the Canal Zone, where breeding takes place from May through January. In the wet Pacific lowlands of the Golfo Dulce region in Costa Rica, breeding begins as early as March.

Males of *Hyla ebraccata* usually call from the leaves of emergent herbs or from the leaves of bushes and trees closely overhanging the water in temporary ponds in, or at the edge of, forest. Observations on small choruses indicate that individual males answer to one another's call. The chorus structure seems to be organized into duets. However, in large choruses, this organization is either non-existent or is not apparent.

In the breeding season, the frogs secrete themselves by day amidst herbaceous plants growing in or around the breeding ponds. Individuals have been found in bromeliads both in the rainy and in the dry seasons.

The eggs are deposited on the dorsal surfaces of leaves, usually of herbaceous plants, above the water. All eggs are in a single layer on the leaf. The external membranes are barely visible, for the eggs consist of a single coherent mass. Eggs in the yolk plug stage have diameters of 1.2 to 1.4 mm. Seventeen masses of eggs were found at Toocog, El Petén, Guatemala, between June 30 and July 2, 1960. These masses contained from 24 to 76 (mean, 44) eggs. The jelly is extremely viscous and tacky to the touch. At time of hatching, the jelly becomes less viscous; the tadpoles wriggle free of the jelly and continue to wriggle across the surface of the leaf until they reach the edge and drop into the water. Hatchling tad-

poles are active swimmers and have only a small amount of yolk. Larger tadpoles inhabit shallow weedy parts of ponds and take refuge in dense aquatic vegetation.

REMARKS: Duellman (1966b) showed that *Hyla weyeri* Taylor is nothing more than a color variant of *Hyla ebraccata* Cope. He concluded that only one species is involved, because both color variants were found breeding in the same pond the same night and that no differences were discernible in the mating call. Furthermore, the "*weyeri*" color pattern (pl. 49, fig. 8) is present on both the Caribbean and Pacific lowlands of lower Central America and in the Gulf lowlands of México.

Dunn (1931b, and 1933) and Breder (1946) used the name *Hyla leucophyllata* (Bereis) for Panamanian frogs currently assigned to *Hyla ebraccata*. On the basis of our present knowledge of this variation within species in the *Hyla leucophyllata* group, I am convinced that *leucophyllata* and *ebraccata* are not conspecific. *Hyla ebraccata* differs from *leucophyllata* in having a white or yellow labial mark expanded below the eye; the lips of *Hyla leucophyllata* are uniform brown.

ETYMOLOGY: The specific name *ebraccata* is derived from the Latin *bracatus* meaning "wearing trousers" and from the Latin prefix *e-*; the name means literally "without trousers" and refers to the unpigmented condition of the thighs.

DISTRIBUTION: *Hyla ebraccata* inhabits the Caribbean and Gulf lowlands of southern México, exclusive of the Yucatan Peninsula, but occurs in British Honduras and the south-

ern part of El Petén, Guatemala. The species has not been found in Honduras, and only two specimens are known from Nicaragua. The species is abundant on the Caribbean lowlands of Costa Rica and Panamá eastward to the Canal Zone, where it crosses onto the Pacific lowlands of eastern Panamá and the Chocó of Colombia. A disjunct population occurs in the Golfo Dulce region in the Pacific lowlands of Costa Rica (fig. 95). Most of the localities from which this species is known are on the lowlands or low foothills, but at some places, *Hyla ebraccata* occurs at moderate elevations. For example, it occurs at 800 meters at Laguna, Darién Province, Panamá, and at Tilarán, Guanacaste Province, Costa Rica; the highest known elevation is 1200 meters at Moravia de Turrialba, Cartago Province, Costa Rica.

See Appendix 1 for the locality records of the 1258 specimens examined.

The *Hyla parviceps* Group

DEFINITION: The members of this group are small species; males attain a maximum snout-vent length of 24 mm. and females, 31 mm. The dorsum is variously marked with dark brown; a creamy white canthal stripe and subocular marks are usually present. The thighs have conspicuous yellow or orange spots bordered by brown or black. Females characteristically have a broad pale tan, creamy yellow, or white dorsolateral stripe. Dermal folds and appendages are lacking on the limbs; a short axillary membrane is present. Males have a single, median, subgular vocal sac and lack nuptial excrescences on the pollices. The cranial elements are weakly os-

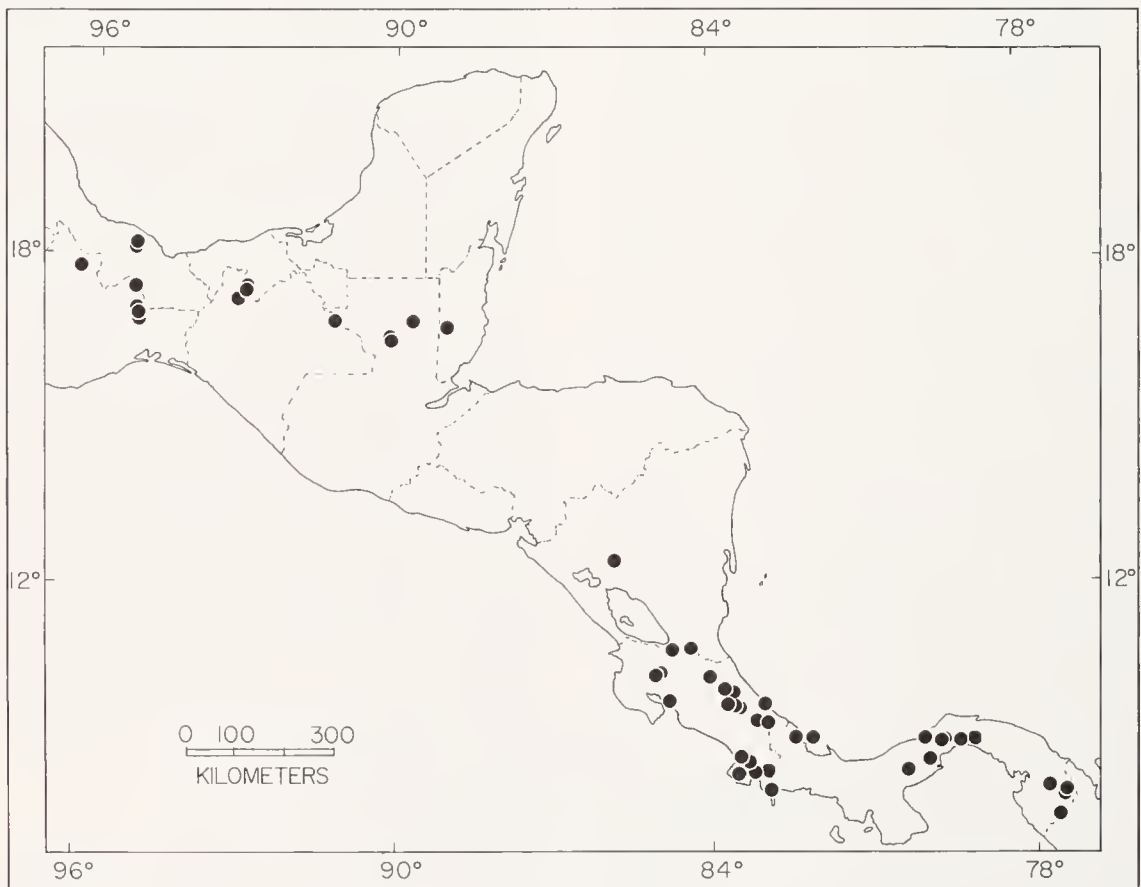


FIG. 95. Distribution of *Hyla ebraccata*.

sified; a large frontoparietal fontanelle is present (fig. 96). The quadratojugal is greatly reduced and not in contact with the maxillary; the anterior arm of the squamosal is short and does not extend to the maxillary. The nasals are relatively small, rectangular, separated medially, but in contact with the sphenethmoid. Prevomerine teeth are present. The tadpoles have xiphicercal tails and terminal mouths lacking teeth. The mating call consists of a short trill. The haploid number of chromosomes is 15 (known in *H. rondoniae* and *subocularis*).

COMPOSITION: Five nominal species belong to this group. Only one species, *Hyla subocularis*, occurs in Central America; the other species are South American. Of the single Central American species, 62 preserved specimens, three skeletons, and one lot of tadpoles have been examined.

COMMENTS: Of the eight known species in this group, *Hyla parviceps* is distinctive in having a dark gray or black belly and a bright orange spot on the ventral surface of each shank. The other species lack the orange spot, have a creamy-white venter, and have more distinctive subocular markings. Of the latter

group, *Hyla luteocellata* Roux is known only from northern Venezuela, and *H. grandisonae* Goin is known only from Guyana, whereas *Hyla rondoniae* Bokermann and *H. bokermanni* Goin are known from the upper Amazon Basin, the region inhabited by *Hyla parviceps* Boulenger. *Hyla bokermanni*, *rondoniae*, and *parviceps* occur sympatrically in Napo Province, Ecuador. *Hyla microps* occurs in eastern Brasil, and *H. carnifex* is known from the Pacific slopes of Ecuador.

Hyla subocularis apparently is a post-Pliocene invader in Central America from a diverse and widely distributed group in South America. The affinities of the *Hyla parviceps* group seem to be with the *Hyla leucophyllata* group and more distantly with the *Hyla microcephala* group.

Hyla subocularis Dunn

Hyla subocularis Dunn, 1934, p. 2 [holotype, A.M.N.H. No. 41117 from the Río Chucumaque at the first creek above the Río Tuquesa, Darién, Panamá; Charles M. Breder, Jr. collector].

DIAGNOSIS: This small species differs from all other Middle American hylids by having the thighs unpigmented except for a bright yellow spot bordered by black and by having the following markings on the head; a creamy white or creamy yellow vertical, narrow, rostral stripe connected to a narrow stripe which is continuous along the edge of the eyelid with a stripe above the tympanum, and two vertical white or yellow bars from the eye to the edge of the lips. *Hyla parviceps* differs from *subocularis* by having black thighs with creamy yellow streaks, a dark venter, one or two small yellow labial spots, and by lacking the narrow stripes on the head. *Hyla rondoniae* resembles *subocularis*, but differs in having brown thighs with two creamy yellow round spots. See the section on Remarks for comments on *Hyla bokermanni* and *luteocellata*.

DESCRIPTION: This is a small frog; males attain a maximum snout-vent length of 23.1 mm. (mean, 25 specimens from Tacarcuna, Darién, Panamá, 21.7 mm.), and females reach 26.1 mm. (mean, six specimens, 24.8 mm.). In the sample of 25 males from Tacarcuna, the ratio of tibia length to snout-vent length is 0.481 to 0.552 (mean, 0.508); the ratio of foot length to snout-vent length is

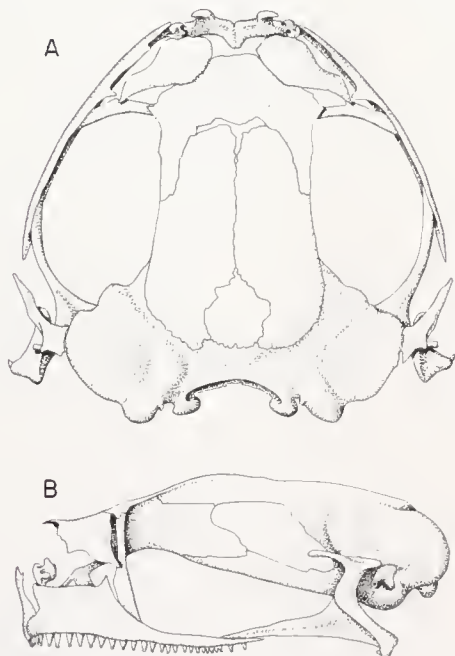


FIG. 96. Dorsal (A) and lateral (B) views of the skull of *Hyla subocularis*, K.U. No. 77690. $\times 7$.

0.381 to 0.450 (mean, 0.426); the ratio of head length to snout-vent length is 0.290 to 0.336 (mean, 0.319); the ratio of head width to snout-vent length is 0.316 to 0.341 (mean, 0.327), and the ratio of the diameter of the tympanum to that of the eye is 0.259 to 0.440 (mean, 0.366). Females have proportionately larger heads and larger tympani. In the sample of six females from Tacarcuna, the ratio of head length to snout-vent length is 0.314 to 0.335 (mean, 0.327); the ratio of head width to snout-vent length is 0.330 to 0.344 (mean, 0.340), and the ratio of the diameter of the tympanum to that of the eye is 0.355 to 0.481 (mean, 0.413).

The head is about as wide as the body, and the top of the head is flat or slightly convex. In dorsal and lateral profiles the snout is truncate; in lateral profile the snout slopes slightly posteroventrally. The snout is relatively short; the nostrils are barely protuberant and are situated about three-fourths the distance from the eyes to the tip of the snout. The canthus is rounded, but distinct; the loreal region is barely concave, and the lips are moderately thin and barely flared. There is no distinct dermal fold extending posteriorly from the eye. The tympanum is rather indistinct, situated posterior to the eye, and separated from the eye by a distance equal to about one and one-half times the diameter of the tympanum.

The arm is moderately long; the forearm is more robust than the upper arm. An abbreviated axillary membrane is present. There is no dermal fold along the outer edge of the forearm, but a faint transverse fold is present on the wrist. The fingers are short and broad and have relatively large discs; the diameter of the disc on the third finger is about equal to the diameter of the tympanum. The subarticular tubercles are relatively small and round; the distal tubercle on the fourth finger is bifid in about one-third of the specimens. The supernumerary tubercles are small, round, indistinct, and arranged in a single row on the proximal segments of the second, third, and fourth fingers. The prepollex is slightly enlarged; breeding males lack horny nuptial excrescences. The fingers are about one-third webbed (fig. 97A). The webbing is vestigial between the first two fingers but connects the base of the penultimate phalanx of the second

finger to the base of the antepenultimate phalanx of the third and continues from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels barely overlap. The tibiotarsal articulation extends to the anterior corner of the eye. There is no tarsal fold. The inner metatarsal tubercle is low and elliptical, and the outer metatarsal tubercle is absent. The toes are moderately long and slender; the discs are slightly smaller than those of the fingers. The subarticular tubercles are small and round; a few supernumerary tubercles are present on the proximal segments of all but the first toe. The toes are about two-thirds webbed (fig. 97B). The webbing connects the first two toes at the bases of the penultimate phalanges; the web extends from the middle of the penultimate phalanx of the second toe to the base of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the level of the upper edges of the thighs. The anal sheath is short and broad. The skin is moderately granular on the belly and ventral surfaces of the thighs; elsewhere it is smooth. A thin thoracic fold is present. The tongue is ovoid, slightly longer than wide, very shallowly notched anteriorly and posteriorly, and barely free behind. In males, there are two or three (mean, 2.4) and females, three to five (mean, 3.4) prevomerine teeth situated on distinct transverse elevations between the posterior margins of the small, round choanae. The vocal slit extends from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla subocularis* is yellowish tan with brown dorsal and lateral markings and one or more black-bordered yellow spots on the anterior or anterodorsal surfaces of the thighs (pl. 49, fig. 6). The dorsum is yellowish tan or pale brown, usually with an X-shaped mark centered in the scapular region; the anterior arms of the X extend onto the eyelids, and the posterior arms are

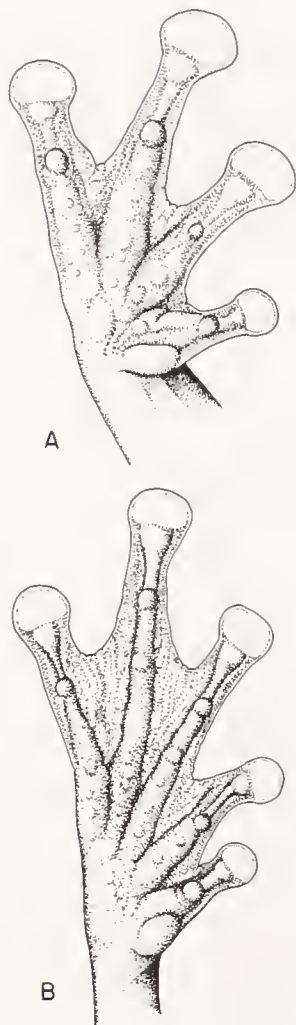


FIG. 97. Hand (A) and foot (B) of *Hyla subocularis*, K.U. No. 77355. $\times 7$.

continuous, or not, with a pair of short brown streaks in the sacral region. Usually a short middorsal brown streak is present posterior to the sacrum. The dorsal surfaces of the arms, the shanks, and the feet are pale tan with brown transverse bars, usually two or three bars on the forearm and four or five bars on the shank. In some individuals, dark brown or black flecks are scattered on the dorsum of the body, forearm, and shanks. The side of the head and anterior part of the flanks are dark brown. A creamy yellow vertical rostral stripe connects with a similarly colored canthal stripe, which extends along the outer edge of the eyelid and continues posteriorly

above the insertion of the forearm and fades into the dorsal coloration in the mid-flank region. In females, the stripe is widened above the forearm and extends posteriorly to the mid-flank region as a broad, creamy tan stripe. Usually two, but sometimes only one, vertical, creamy white or creamy yellow suborbital bars are present. In most individuals both bars reach the orbit, and in some specimens, the bars are expanded at the edge of the lip. In a few individuals the bars are fused ventrally to form a short labial stripe. The proximal surfaces of the upper arm, the posterior parts of the flanks, and the thighs lack pigment, except for distinctive markings on the thighs. Usually one, but sometimes two, bright yellow spots are present on the antero-dorsal surfaces of the thighs; these spots are bordered with black pigment, which in some specimens forms a reticulate pattern on the posterior surfaces of the distal part of the thighs. In most specimens, there is a small yellow, black-bordered spot in the groin and a dark brown or black mark at the insertion of the hind limb. The belly is white; the chin and throat are creamy white. In some specimens, brown flecks or spots are present along the edge of the lower lip. The ventral surfaces of the limbs and the webbing on the hands and feet lack pigment. The iris is pale silver peripherally and rose-pink medially. The palpebral membrane is unpigmented.

In preservative, the dorsum is grayish brown with dark brown markings. The dorso-lateral stripe in females is creamy white and the narrow stripes on the head in both sexes are creamy white. The distinctive markings on the thighs are pale tan or white surrounded by black. The venter is creamy white.

TADPOLES: A single tadpole in developmental stage 37 has a total length of 27.5 mm. and a body length of 9.1 mm. The body is broader than deep. In dorsal profile, the snout is broad and bluntly rounded, in lateral profile it is round. The eyes are large, widely separated, and directed laterally. The nostrils are directed anterolaterally at a point about two-thirds of the distance from the eyes to the snout. The opening of the sinistral spiracle is directed posteriorly at a point below the midline and about two-thirds of the distance from the snout to the posterior end of



FIG. 98. Tadpole of *Hyla subocularis*, K.U. No. 116784. $\times 5$.

the body. The anal tube is dextral and short. The caudal musculature is slender and extends well beyond the end of the fins so as to form a xiphicereal tail. The dorsal fin is slightly deeper than the ventral fin, does not extend onto the body, and at midlength of the tail is half again as deep as the caudal musculature (fig. 98).

The body and tail are black with a dorso-lateral tan stripe on the body and irregular tan vertical marks on the tail. Small bronze spots are present on the venter. The iris is orange-red with black flecks. In preservative, the coloration remains the same, except for the loss of the color of the iris.

The mouth is small and terminal. The upper lip is bare, and the rest of the mouth is bordered by a single irregular row of large blunt papillae. The beaks are massive and rounded with fine serrations. Teeth are absent (fig. 99).

MATING CALL: The call of *Hyla subocularis* is a short trill. Two recordings obtained at Tacarcuna, Darién Province, Panamá, show that there is a call repetition rate of three to 20 seconds. The duration of the trill is 0.53 of a second, and the trill has a pulse rate of 43 pulses per second and a dominant fre-

quency of 2200 cycles per second (pl. 29, fig. 2).

NATURAL HISTORY: *Hyla subocularis* has been found in areas of humid forest. At Tacarcuna, Darién Province, Panamá, the species was found breeding in July, 1963. Males were calling from leaves of low trees and bushes overhanging the pond and from horizontal leaves of emergent herbaceous vegetation in the pond. Claspings pairs were found on emergent vegetation. Unlike *Hyla ebraccata*, which was abundant in the ponds where *subocularis* was breeding, the latter species apparently does not spend the day hidden amidst vegetation in the pond. At dusk, many individuals of *Hyla subocularis* were observed moving towards the pond on several consecutive nights when there did not seem to be any increase in breeding activity in this species.

A recently metamorphosed young was found on an herb next to a pond at Laguna, Darién Province, on July 6, 1963; another was found on a bush above a pond at Tacarcuna, on July 13. These specimens have snout-vent lengths of 11.5 and 11.9 mm. In life, the dorsum was pale bronze-tan; yellow and black pigment were not present on the thighs. The iris was silver peripherally and red medially.

Charles W. Myers obtained two tadpoles of this species on November 25, 1965, in shallow water in a swamp forest about 7 kilometers upstream on the Río Ucurganti from the Río Chucunaque in Darién Province, Panamá. The tadpoles were resting on leaves on the bottom. The caudal musculature posterior to the fins was observed to wiggle conspicuously. One tadpole was preserved on December 3, 1965, in developmental stage 37 (figs. 98 and 99), and the other metamorphosed on December 6.

REMARKS: Breder (1946, p. 417) listed three specimens in addition to the holotype. One of these, A.M.N.H. No. 51777 from Río



FIG. 99. Mouth of tadpole of *Hyla subocularis*, K.U. No. 116784. $\times 45$.

Chucumaque is a juvenile *Hyla subocularis*; A.M.N.H. No. 51784 is a young *Hyla rosenbergi*, and A.M.N.H. No. 51786 is a series of juvenile *Eleutherodactylus* and recently metamorphosed hylids, none of which seem to be *Hyla subocularis*.

On the basis of observations of living individuals in the field, I suspect that *Hyla bokermanni* and *H. subocularis* are conspecific. Goin (1960c) named *Hyla bokermanni* on the basis of an immature female from Tarauaca, Acre, Brasil, and Cochran and Goin (1970) recorded the species from Río Manso, Córdoba, Colombia. I have examined four of the specimens (C.J.G. Nos. 2355-2358) from the Río Manso and find that they are indistinguishable from Panamanian *Hyla subocularis*. I collected individuals conforming to descriptions given by Goin (1960c) at Santa Cecilia, Napo Province, Ecuador. In life these individuals had bright yellow, black-bordered spots on the thighs, the same pattern of creamy yellow lines on the head as noted in Panamanian *Hyla subocularis*, and an iris that was red medially and silver peripherally. The frogs at Santa Cecilia were readily distinguished from *Hyla parviceps*, which lacks the rostral, canthal, and supratympanic stripes and black-bordered yellow spots on the thighs and has black limbs with a bright orange spot on the ventral surface of the shank. The third species in the *parviceps* group occurring at Santa Cecilia is *Hyla rondoniae*, described by Bokermann (1963) from Rondonia, Brasil. In this species the markings on the head are like those in *Hyla subocularis*, but the coloration of the thighs differs; the thighs are brown with usually two creamy yellow spots (fused into an elongate mark in some individuals) on the anterodorsal surface of the thigh. The call of *Hyla rondoniae* is similar to that of *subocularis* in structure; analysis of one recording obtained at Santa Cecilia reveals that each note has a duration of 0.44 of a second, a pulse rate of 35 pulses per second, and a dominant frequency of 4200 cycles per second. Thus the call is slightly shorter and more slowly pulsed, but noticeably higher pitched than that of *Hyla subocularis*.

ETYMOLOGY: The specific name *subocularis* is derived from the Latin *sub*, meaning under, and *ocularis*, meaning of the eyes, and

refers to the distinctive vertical creamy yellow bars beneath the eyes.

DISTRIBUTION: *Hyla subocularis* is known from the lowlands to elevations of about 800 meters in the Chucumaque-Tuira Basin (Pacific drainage), in Darién Province, Panamá, and the Río Manso, Departamento Córdoba, Colombia (fig. 100).

See Appendix 1 for the locality records of the 66 specimens examined.

The *Hyla albomarginata* Group

DEFINITION: The members of this group are medium-sized tree frogs; males attain a maximum snout-vent length of 54 mm. and females, 60 mm. The dorsum is green (creamy white or pale yellow in preservative) with scattered dark flecks and/or small white spots. The webbing and/or hidden surfaces of the hind limbs are pink or red. The palpebral membrane is clear. The fingers are about half, and the toes about three-fourths webbed. A tarsal fold is present, and some species have

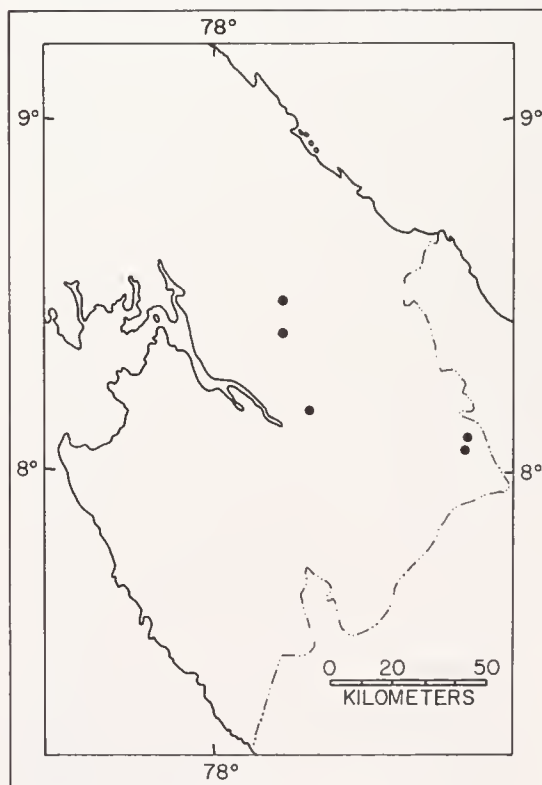


FIG. 100. Distribution of *Hyla subocularis*.

a dermal flap on the heel. An axillary membrane is absent. Males have a single, median, subgular vocal sac and a protruding prepollex, which does not bear a horny nuptial exerescence but through which a prepollical spine projects in some species. The skull is only moderately ossified; an ovoid frontoparietal fontanelle is present (fig. 101). The sphenethmoid is moderately well ossified, whereas the nasals are poorly ossified, long, slender elements, which are narrowly separated medially and have a cartilaginous connection to the sphenethmoid. The nasals bear slender maxillary processes which do not articulate with the maxillaries. The premaxillaries are delicate and have short alary processes. The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosal extends no more than half of the distance to the maxillary. The prevomers are not completely ossified anteriorly but have well-developed angular dentigerous processes (fig. 101). The palatines and parasphenoid are delicate, but the pterygoids are robust and articulate with the prootics and broadly with the maxillaries. The known tadpoles are pond types and have robust bodies and moderately large mouths with two upper and four lower rows of teeth. The known mating calls consist of a series of short, well-modulated notes. The haploid number of chromosomes is 12 (known only in *Hyla rufitela*).

COMPOSITION: Nine species presently are included in this group; only one species (*Hyla rufitela*) occurs in Central America. Of the others, *Hyla albomarginata* is widespread in the tropics of South America east of the Andes, *pellucens* occurs on the Pacific lowlands of Ecuador, *albopunctulata* occurs in the upper Amazon Basin, and five species (*albofrenata*, *albolineata*, *albosignata*, *musica*, and *prasina*) occur in southeastern Brasil. Eighty-three preserved frogs, one skeleton, nine lots of tadpoles, and one preserved clutch of eggs of the Middle American species have been examined.

COMMENTS: This predominantly South American group possibly is related to the *Hyla granosa* group; both groups have angled dentigerous processes of the prevomers, projecting prepollical spines, and a green dorsum. Two other South American groups—the *Hyla*

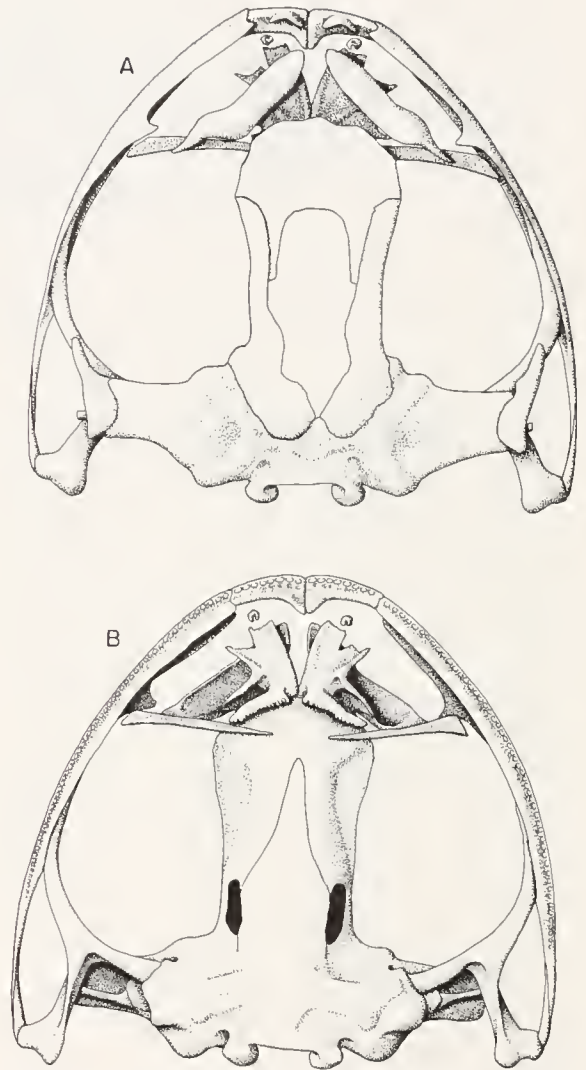


FIG. 101. Dorsal (A) and ventral (B) views of the skull of *Hyla rufitela*, K.U. No. 77662. $\times 5$.

boans group and the *Hyla geographica* group—also have projecting prepollices and strongly angular dentigerous processes of the prevomers; members of those groups are medium to large in size and have a tan or brown dorsum. The relationships of these widespread South American groups are obfuscated by a dearth of information on tadpoles, life histories, and behavior.

Hyla rufitela Fouquette

Hyla albomarginata: Boulenger, 1882a, p. 356. Günther, 1901 (1885-1902), p. 284. Taylor, 1952c, p. 893.

Hyla rufitela Fouquette, 1961a, p. 595 [holotype, F.M.N.H. No. 13053 from Taylor Swamp, Barro Colorado Island, Canal Zone, Panamá; Karl P. Schmidt collector].

DIAGNOSIS: This medium-sized green frog has red webs and a projecting propollex, a combination of characters that distinguishes it from all other Middle American hylids. *Hyla loquax* and *H. pseudopuma infucata* have red webbing but lack a projecting propollex; furthermore, both of those species are brown or gray dorsally. Other species of Middle American hylids having projecting prepollices differ from *rufitela* in a variety of characters—*Plectrohyla* lacks red color and has little webbing on the hand; the *Hyla boans* group has no red but has dark reticulations or vertical bars on the flanks and thighs, and the *Hyla miliaria* group has extensive dermal fringes on the limbs and fully webbed hands and feet.

DESCRIPTION: Males of this medium-sized species attain a maximum snout-vent length of 49.2 mm., and females reach 52.6 mm. In a series of 25 males from Barro Colorado Island and Achioté, Panamá, the snout-vent length is 41.2 to 49.2 (mean, 46.2) mm.; the ratio of tibia length to snout-vent length is 0.482 to 0.558 (mean, 0.521); the ratio of foot length to snout-vent length is 0.359 to 0.418 (mean, 0.391); the ratio of head length to snout-vent length is 0.333 to 0.368 (mean, 0.356); the ratio of head width to snout-vent length is 0.333 to 0.362 (mean, 0.349), and the ratio of the diameter of the tympanum to that of the eye is 0.462 to 0.638 (mean, 0.546). Two females from the same area have snout-vent lengths of 49.6 and 52.6 mm. They differ from the males only by having slightly larger tympani; the ratio of the diameter of the tympanum to that of the eye is 0.510 and 0.652.

The head is slightly narrower than the body, and the top of the head is flat. In dorsal profile, the snout is acutely rounded but truncate terminally; in lateral profile, the snout is rounded above and slightly posteroventrally inclined below. The snout is long; the slightly protuberant nostrils are situated at a point about five-sixths of the distance from the eyes to the tip of the snout. The canthus is angular, and the loreal region is noticeably concave; the lips are moderately thick and barely flared. A thin dermal fold extends posteriorly

from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately short and robust; an axillary membrane is absent. There is no row of tubercles on the ventrolateral edge of the forearm, but a weak transverse dermal fold is present on the wrist. The fingers are rather short and robust and bear moderately large discs; the width of the disc on the third finger is approximately equal to the diameter of the tympanum. The subarticular tubercles are moderate in size and subconical; the distal tubercle on the fourth finger is weakly bifid in some individuals. No distinct supernumerary tubercles are evident, and a true palmar tubercle is absent. The propollex is moderately enlarged and in males is strongly protuberant; in some males a spine projects from the tip of the prepollical process. There is no nuptial excrecence. The fingers are about one-half webbed (fig. 102A). The webbing is vestigial between the first and second fingers and extends from the distal end of the penultimate phalanx of the second to the distal end of the penultimate phalanx of the third and on to the base of the disc of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to a point between the eye and nostril. Two or three small tubercles and a thin transverse dermal fold are present on the heel. The tarsal fold is weak, present only distally, or not evident at all. The inner metatarsal tubercle is long, low, flat, elliptical, and distinctly visible from above. A small subconical outer metatarsal tubercle is evident in some specimens. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are rather large and round; the supernumerary tubercles are small and for the most part, indistinct. The toes are about three-fourths webbed (fig. 102B). The webbing extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second

to the distal end of the antepenultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

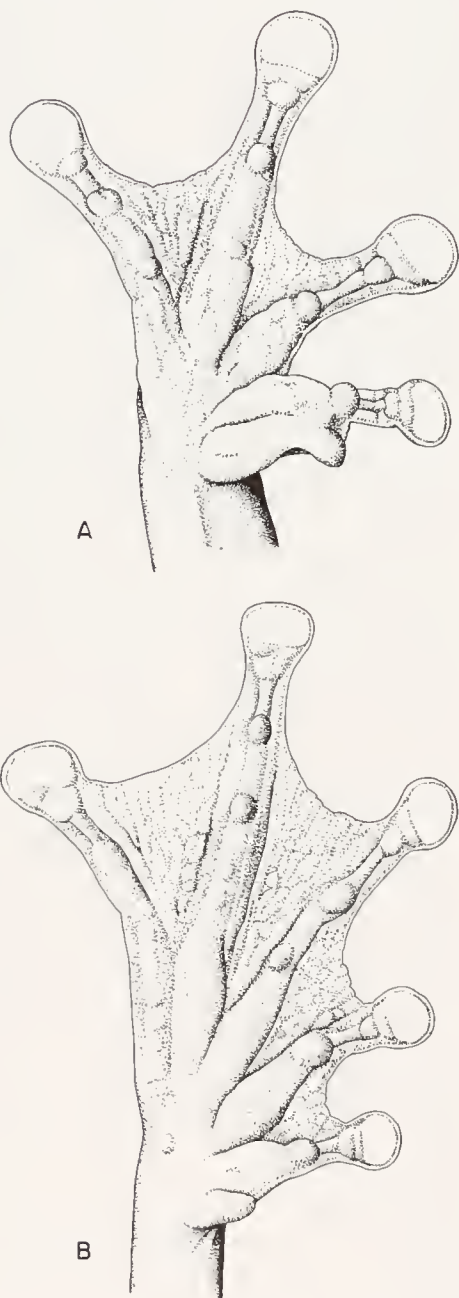


FIG. 102. Hand (A) and foot (B) of *Hyla rufitela*, K.U. No. 108855. $\times 4.5$.

The anal opening is directed posteriorly at the upper level of the thighs. A short, broad anal flap is present. A pair of vertical dermal folds and numerous tubercles are present below the anal opening. The skin on the chest, belly, and proximal posteroventral surfaces of the thighs is granular, elsewhere the skin is smooth. The tongue is elongate, widest anteriorly, shallowly notched or not behind, and not free posteriorly. The dentigerous processes of the prevomers are long anteromedially inclined, narrowly separated ridges between the large triangular choanae. In many individuals, the anteromedial part of each dentigerous process is angled to lie in a transverse position. Males have nine to 12 teeth on each process and a total of 18 to 23 (mean, 21.3) prevomerine teeth; females have 10 to 12 teeth on each process and a total of 21 to 23 (mean, 22.0) prevomerine teeth. The vocal slits are long and extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Hyla rufitela* consists of a green dorsum with darker flecks and occasional white spots and red webbing (pl. 50, fig. 1). The dorsal surfaces of the body and limbs are green with small black or brown flecks and small silvery white spots. The flanks are yellowish olive, and the axilla and groin are pale blue or bluish green. The anterior and posterior surfaces of the thighs are pale green, except that usually the distal half of the posterior surfaces of the thighs is tomato red. The webbing on the hands and feet is red. A greenish white stripe is present on the ventrolateral edge of the forearm. The throat and ventral surfaces of the limbs are pale green, and the belly is creamy yellow medially and greenish white laterally. The iris is silvery bronze.

Little variation occurs in coloration. In some individuals, a faint greenish white stripe is present on the outer edge of the foot or on the supratympanic fold. The red area on the posterior surfaces of the thighs varies from a small dash of red distally to nearly covering the entire posterior surface.

In preservative, the dorsum is creamy tan with many small brown flecks; in some individuals the flecks are coalesced into small

spots. The flanks and ventral surfaces are creamy white. In some specimens preserved for five years, the red is still evident on the posterior surfaces of the thighs and on the web.

TADPOLES: A series of tadpoles is available from Barro Colorado Island, Panamá and from Golfito and 4.5 kilometers west of Rincón de Osa, Puntarenas Province, Costa Rica. The largest tadpole from the latter locality is in developmental stage 40 and has a total length of 57 mm. A typical tadpole in developmental stage 37 has a body length of 19.1 mm. and a total length of 54.8 mm. The body is robust and wider than deep. In dorsal profile, the body is truncate posteriorly, and the snout is rounded; in lateral profile the snout slopes anteroventrally from the eyes to a round tip. The eyes are moderately large, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point just below the midline about two-thirds of the distance from the tip of the snout to the posterior edge of the body. The anal tube is long and dextral. The caudal musculature is rather slender and extends nearly to the tip of the pointed tail. The dorsal fin is high, deepest slightly anterior to the midlength of the tail, and not extending on to the body. The ventral fin is relatively shallow and deepest at a point about two-thirds of the length of the tail. At midlength of the tail, the depth of the caudal musculature is about equal to the depth of the ventral fin but noticeably less than the depth of the dorsal fin (fig. 103).

The body is olive-tan with green and tan lichenous markings on the flanks. The belly is white with silvery flecks. The caudal musculature

is orange-tan with dark brown markings. The iris is bronze. In preservative, the dorsum is mottled tan and dark brown with overlying small dark brown flecks. The venter lacks pigment. The caudal musculature is creamy tan. Numerous small round blotches are present on the caudal musculature. The dark pigment tends to form transverse bands on the dorsum of the musculature. Small brown flecks and reticulations are present on the dorsal fin and on the posterior half of the ventral fin.

The mouth is ventral and relatively small; its width is equal to about one-third of the greatest width of the body. The median part of the upper lip is bare; the rest of the lip is bordered by a single row of elongate papillae. Deep lateral folds are present in the lip. The beaks are slender and bear short, conical serrations. The upper beak is in the form of a broad arch with long, slender, terminally expanded lateral processes; the lower beak is very broadly V-shaped and slender. There are two upper and four lower rows of teeth. The upper rows are equal in length, and the second upper row is narrowly interrupted medially. The lower rows are complete; the first three rows are approximately equal in length but somewhat shorter than the upper rows, whereas the fourth lower row is noticeably shorter (fig. 104).

A developmental series of tadpoles was obtained from a clutch of eggs on Barro Colorado Island, Panamá. The eggs hatched on June 8, 1963. The average length of the body of hatchlings is 2.7 mm., and the tail length is 5.0 mm. These tadpoles are in developmental stage 20; the cornea is not visible, and the oral suckers are well developed. There is a large yolk sac and short, many-stalked gills. Tadpoles after five days were in developmental stage 25 and had a functional spiracle and



FIG. 103. Tadpole of *Hyla rufitela*, K.U. No. 104300. $\times 2$.

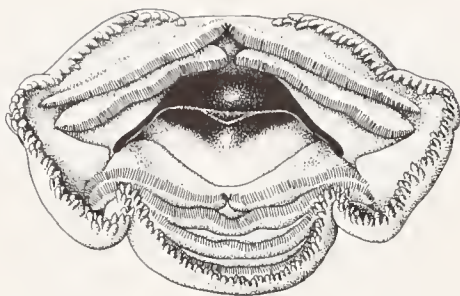


FIG. 104. Mouth of tadpole of *Hyla rufitela*, K.U. No. 104300. $\times 15$.

eyes; the gills and oral suckers were lost. The beaks are formed, and two upper and two lower rows of teeth are present in these tadpoles which have an average body length of 3.7 mm. and a total length of 9.7 mm. Dark pigment is present on the dorsum and forms transverse bands on the dorsal surface of the caudal musculature. After 16 days, the tadpoles were still in developmental stage 25 but had developed the four lower rows of teeth. The average body length is 3.9 mm., and the total length is 11.1 mm. After 28 days the average length increased to 4.9 mm., and the total length to 12.7 mm. In these tadpoles, pigment is present anteriorly on the dorsal fin. At an age of 32 days, the tadpole is still in developmental stage 25 and has an average body length of 5.5 mm. and a total length of 15.3 mm. Definite flecks are present on the dorsal and ventral fins and the pigmentation extends ventrolaterally on the body.

MATING CALL: The call of *Hyla rufitela* consists of a series of clucks. Three different individuals produced call groups having nine, 11, and 21 notes per call group. The note repetition rate varies from 22 to 63 (mean, 38) notes per minute. Seven to nine harmonics are evident in the notes (pl. 23, fig. 3). Each note has a duration of about 0.05 of a second. The fundamental frequency is at about 400 cycles per second; the dominant frequency usually is the third harmonic at about 1600 cycles per second. The second and fourth harmonics are also emphasized. In many of the notes there is a rise in pitch towards the end of the note.

Fouquette (1961a, p. 599) noted that the notes in some individuals were followed by a guttural trill, which he suggested was probably a "warm-up" call. Observations on calling

males indicate that the normal note is produced by a rapid expansion of the vocal sac; sometimes, this complete expansion is followed by a series of quick pulsations of the vocal sac. I do not believe that this is a "warm-up" call.

NATURAL HISTORY: *Hyla rufitela* inhabits tropical rain forests; apparently the species is active throughout most of the year. Dunn (1931b, p. 414) reported this species calling on Barro Colorado Island in August. Noble (1918, p. 343) reported a gravid female from Maselina Creek on August 16. Charles W. Myers observed breeding activity at the Río Cahuita, Veraguas Province, Panamá, on October 26, 1966, and on Cayo de Agua, Bocas del Toro Province, Panamá, on November 2, 1964. I have found calling males on Barro Colorado Island and at Achioté, Colón Province, Panamá, in June and on the Peninsula Valiente, Bocas del Toro Province, Panamá, in March.

Males usually call from dense vegetation and secluded places just above standing water in swamp forest. On Barro Colorado Island and at Achioté, the preferred calling sites were in thickets of the pita plant, *Aechmea* (= *Ananas*) *magdalenae*.

The eggs are deposited as a surface film in shallow water. A clutch of eggs found on Barro Colorado Island on June 6, 1963, was about 15 cm. in diameter. The jelly is clear; the vegetal pole is pale cream and the animal pole is black. The diameter of the eggs is about 1.8 mm., and the diameter of the vitelline membrane is about 2.1 mm. Tadpoles have been found in shallow, vegetation-choked ponds and muddy pools in swamp forests. Two juveniles were metamorphosed from tadpoles obtained at Golfito, Puntarenas Province, Costa Rica on June 18, 1961. The small frogs have snout-vent lengths of 19.7 and 21.5 mm. The dorsum is pale green; the eyelids are brown. There are scattered black flecks on the back. The limbs are yellowish green and the hands and feet are pale yellow. The throat is pale green, and the venter is silvery white. There is no red on the webs or the posterior surfaces of the thighs.

REMARKS: Cope (1886), Noble (1918), Dunn (1931b), and Taylor (1952c) referred Central American specimens of this species to

Hyla albomarginata Spix. Fouquette (1961a) demonstrated the specific distinctness of the Central American specimens from those in the Amazon Basin assignable to *albomarginata*. A considerable hiatus exists between the ranges of these species. *Hyla rufitela* is unknown from eastern Panamá, and *albomarginata* occurs in the Amazon Basin, Guianas, and southeastern Brasil and questionably in the Maracaibo Basin in Venezuela.

ETYMOLOGY: The specific name is derived from the Latin *rufus*, meaning red, and the Latin *tela*, meaning web, and refers to the distinctive red webbing.

DISTRIBUTION: *Hyla rufitela* occurs in rain forest and swamp forest on the Caribbean lowlands at elevations of less than 300 meters from east-central Nicaragua to central Panamá and in the Golfo Dulce region of the Pacific lowlands of Costa Rica (fig. 105).

See Appendix 1 for the locality records of the 94 specimens examined.

The *Hyla boans* Group

DEFINITION: The frogs comprising this group are large species inhabiting lowland forests; in Central America, males attain snout-vent lengths of 131 mm., and females, 117 mm. The dorsum usually is tan or gray with darker irregular blotches and in many specimens a narrow, dark, vertebral line is present. Transverse bars are present on the limbs, and vertical dark lines or reticulations are present on the thighs and flanks in some species. The palpebral membrane is reticulate in one species (*boans*) and clear in the others. The hands are about one-third webbed in one species (*crepitans*) and at least three-fourths webbed in the other species; the feet are at least three-fourths webbed. A strong tarsal fold is present, but an axillary membrane is absent. A dermal appendage is present on the heel in some species (*boans* and *pardalis*). Males have a projecting prepollex and a me-

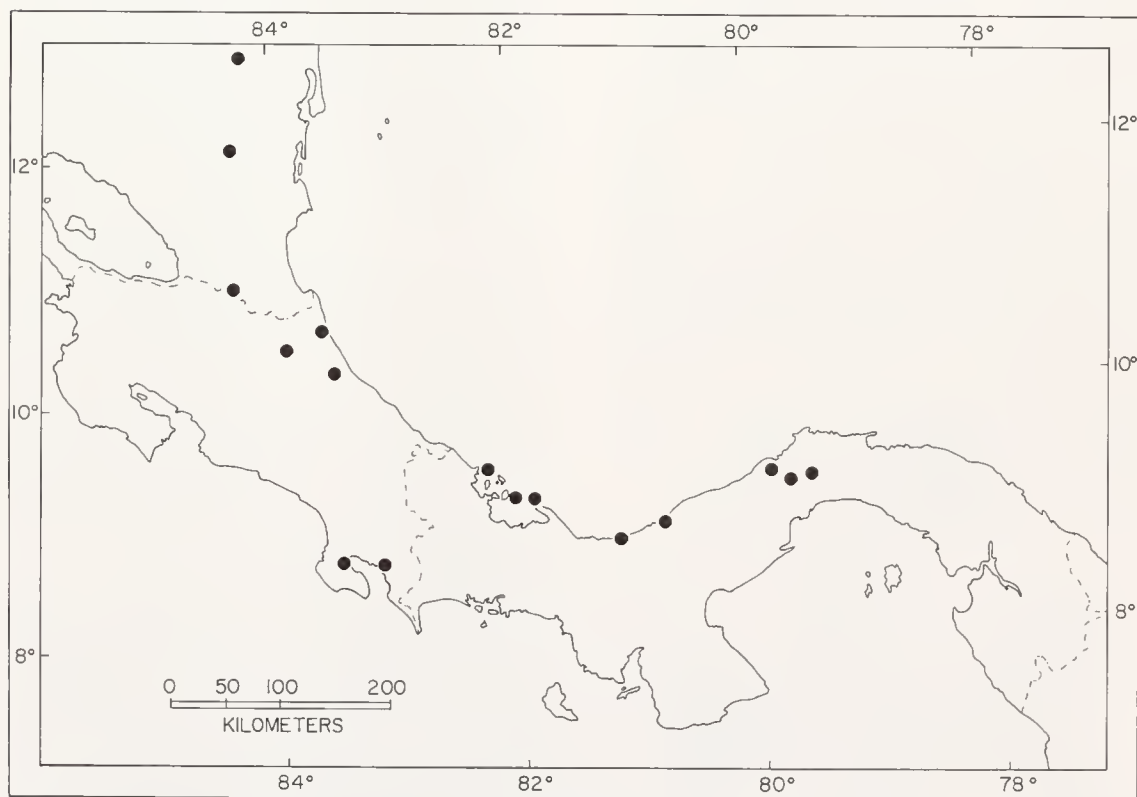


FIG. 105. Distribution of *Hyla rufitela*.

dian subgular vocal sac. The skull is only moderately ossified, and an elongate frontoparietal fontanelle is present (fig. 106). The nasals are slender, weakly ossified, widely separated medially, and have weak maxillary processes. The sphenethmoid is broad and extends anteriorly between the nasals; in the two largest species (*boans* and *faber*) the posteromedian part of the sphenethmoid is depressed and the anterolateral edges are elevated, so as to form distinct canthal ridges. The squamosal is in bony articulation with the crista parotica, and the anterior arm of the squamosal extends about half the distance to the maxillary. The prevomer is large and bears a long, angular, dentigerous process (fig. 106). The palatine is slender, and the pterygoid is well developed and bears a long medial ramus which articulates with the prootic. The tadpoles have robust bodies, moderately deep

caudal fins and small mouths with two upper and four lower rows of teeth. The mating calls consist of low, rather well-modulated short notes resembling the hammering of a stick on a hollow log. The haploid number of chromosomes is 12 (known only in *crepitans*).

COMPOSITION: Seven species are currently recognized in this group; all occur in South America. Two species (*boans* and *crepitans*) are widespread in South America east of the Andes and range into Central America. Another Central American species extends southward on the Pacific slopes to northwestern Ecuador. The other species are strictly South American; *langsdoerffii*, *circundata*, and *faber* are known only from Brasil, whereas *pardalis* extends from Venezuela and the Guianas to southeastern Brasil. Of the three Central American species, 279 preserved frogs, 12 skeletons, seven lots of tadpoles, and one preserved clutch of eggs have been examined.

COMMENTS: Some authors, such as Taylor and Smith (1945, p. 596) have separated this group from *Hyla*. The earlier generic name available for the group is *Boana* Gray, 1825 (genotype, *Rana boans* Linnaeus, 1758). Wagler (1830) designated *Hyla palmata* Daudin, 1803 (= *Hyla boans*) as the type species of *Hypsiboas*, the generic name used by Cope (1867a), who apparently was unaware of Gray's name. Cope (1887, pp. 13-14) include in the genus *Hyla miliaria* Cope, *Hyla xerophyllum* Duméril and Bibron (= *Hyla crepitans* Wied), *Hyla albomarginata* Spix, *Hyla crepitans* Wied (including *Hyla palmata* Daudin), *Hyla crassa* Brocchi, and *Plectrohyla guatemalensis* (Brocchi). Cope obviously based his concept of *Hypsiboas* on the presence of a protruding prepollex and consequently placed together species that are now considered to be members of four groups of *Hyla* and of the genus *Plectrohyla*.

Cochran (1955) placed *crepitans* in the same group as *faber* and *pardalis*, whereas Cochran and Goin (1970) separated *crepitans* from the "maxima" (= *boans*) group apparently solely on the basis of less webbing on the hand in the former. The similarities of other external features, the structure of the skull, the characters of the tadpoles, and the nature of the mating call strongly suggest close phylogenetic relationships.

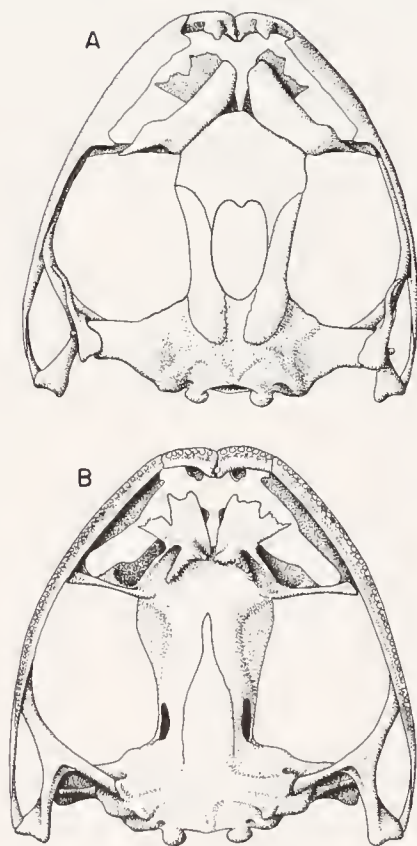


FIG. 106. Dorsal (A) and ventral (B) views of the skull of *Hyla rosenbergi*, K.U. No. 84991. $\times 3$.

Hyla boans, *faber*, and *rosenbergi* have distinctive mating behavior in which the male builds a nest of mud or gravel. I am unaware of any such behavior in *crepitans*, so perhaps this apparent lack of specialized mating behavior in *crepitans* is indicative of more distant relationships with the other species; on the other hand, possibly *crepitans* is the most primitive member of the group. Structurally, the adults of *crepitans* are more generalized than *boans*, *faber*, and *rosenbergi*.

Several evolutionary trends are evident in this group. *Hyla crepitans* has the least developed prepollical spine, whereas the spines are large, pointed, and curved in *boans*, *faber*, *pardalis*, and *rosenbergi* (fig. 107). In the Central American species there is a positive correlation between size and the extent of the webbing on the hands and feet; the smallest species (*crepitans*) has less webbing than *rosenbergi*, which in turn has less than the larger *boans* (figs. 108 and 109). A similar correlation exists with certain parameters of the mating call, such as note repetition rate and duration of notes (table 27).

The differentiation of the *Hyla boans* group undoubtedly occurred chiefly in South America east of the Andes. *Hyla rosenbergi* apparently resulted from the isolation of a

stock of *boans*-like frogs either on the Pacific lowlands of northwestern South America that later moved into Central America or in the Central American lowlands that later moved southward on to the Pacific lowlands of South America. Certainly, the three species in Central America represent three different invasions from South America.

Hyla crepitans Wied

Hyla crepitans Wied, 1824a, pl. 47, fig. 1 [type specimens unknown; type localities given as Tamboril, Jiboya, and Areal da Conquista, Bahia, Brasil]; 1824b, p. 671. Boulenger, 1882a, p. 352. Günther, 1901 (1885-1902), p. 283.

Hypsiboas crepitans: Wagler, 1830, p. 200.

Hyla pugnax O. Schmidt, 1857, p. 11 [holotype, unknown, from "Chiriqui-Flusse unweit Bocca del toro," Panamá (O. Schmidt, 1858, p. 6); J. von Warszewicz collector]. Brocchi, 1882, p. 41.

Hyla xerophylla: Brocchi, 1882, p. 44.

DIAGNOSIS: This moderately large frog has a mottled dorsum, vertical dark lines on the flanks and posterior surfaces of the thighs, a long, low snout, and a protruding prepollex. It differs from other Central American species in the group by having less webbing; the web extends to the base of the disc of the fourth finger in *boans* and *rosenbergi* but only to the distal end of the antepenultimate phalanx in *crepitans*. Furthermore, *crepitans* can be distinguished from *boans* by the absence of a calcar on the heel and the absence of reticulations on the palpebral membrane in *boans*. *Hyla ruftela* differs from *crepitans* by having a green dorsum, unmarked flanks and posterior surfaces of the thighs, red webbing, a weak tarsal fold and much more webbing on the hand. Members of the genus *Plectrohyla* and the *Hyla miliaria* group have protruding pre-



FIG. 107. Palmar view of the right prepollical spine of *Hyla boans*, K.U. No. 104406. $\times 7$.

TABLE 27
Comparison of Certain Parameters, With Means in Parentheses,
of the Mating Calls of Species in the *Hyla boans* Group.

Species	N	Notes per Call Group	Duration of Notes (sec.)	Fundamental Frequency (cps)	Dominant Frequency (cps)
<i>H. crepitans</i>	3	3-5 (4.0)	0.03-0.04 (0.037)	178-185 (182)	965-1288 (1107)
<i>H. rosenbergi</i>	5	2-5 (2.8)	0.06-0.07 (0.062)	130-143 (136)	260-286 (272)
<i>H. boans</i>	3	3-10 (6.0)	0.25-0.28 (0.26)	104-130 (114)	832-910 (869)

pollices; the latter group differs from *Hyla crepitans* by having more webbing and dermal fringes on the limbs. Frogs of the genus *Plectrohyla* have more robust bodies and arms, short heads, and long fingers with small discs.

DESCRIPTION: Males of this moderately large species attain a maximum snout-vent length of 58.5 mm., and females reach 67.9 mm. In a series of 19 males from central Panamá, the snout-vent length is 50.0 to 58.5 (mean, 54.5) mm.; the ratio of tibia length to snout-vent length is 0.531 to 0.583 (mean, 0.556); the ratio of foot length to snout-vent length is 0.378 to 0.413 (mean, 0.397); the ratio of head length to snout-vent length is 0.327 to 0.359 (mean, 0.340); the ratio of head width to snout-vent length is 0.337 to 0.364 (mean, 0.351), and the ratio of the diameter of the tympanum to that of the eye is 0.704 to 0.846 (mean, 0.781). Five females from the same locality have snout-vent lengths of 62.8 to 67.9 (mean, 64.6) mm. They differ from the males in having a proportionately larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.828 to 0.887 (mean, 0.848).

The head is as wide as, or slightly wider than, the body; the top of the head is flat or faintly concave and the eyes are large and prominent. In the dorsal profile the labial border is round, whereas the snout is truncate; in lateral profile the snout is round. The snout is long, and the protuberant nostrils are situated at a point about five-sixths of the distance from the eyes to the tip of the snout. The canthus is slightly elevated and round; the loreal region is barely concave and slopes laterally to the thin, slightly flared lips. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about half of the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. A distinct dermal fold is present on the ventrolateral edge of the forearm, and a weak transverse fold is present on the wrist. The fingers are moderately long and slender and bear relatively small discs; the width of the disc on the

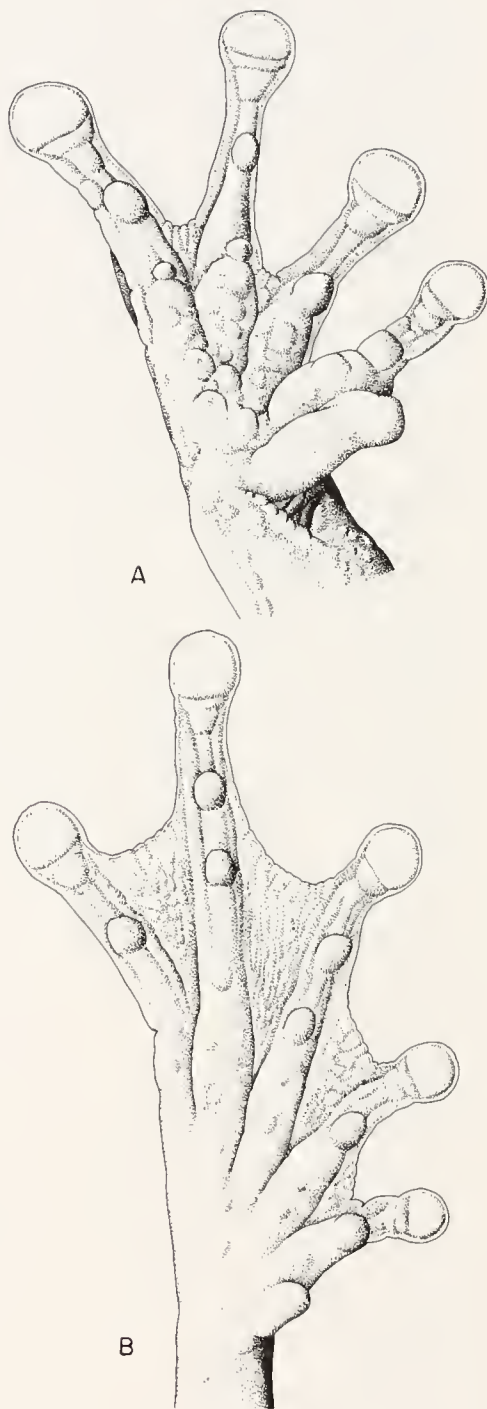


FIG. 108. Hand (A) and foot (B) of *Hyla crepitans*, K.U. No. 77020. $\times 4$.



FIG. 109. Hands and feet of members of the *Hyla boans* group. A and C. *Hyla rosenbergi*, K.U. No. 96065. $\times 2.5$. B and D. *Hyla boans*, K.U. No. 108848. $\times 1.5$.

third finger is slightly greater than half of the diameter of the tympanum. The subarticular tubercles are large and conical; none is bifid. The supernumerary tubercles are low and subconical. No distinct palmar tubercle is evident. In males, the prepollex is greatly enlarged, protuberant, and recurved. In many individuals, the tip of the prepollical spine protrudes through the end of the prepollical eminence. The fingers are about one-third webbed (fig. 10SA). The webbing is vestigial between the first and second fingers, and extends from the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third, and from the middle of the antepenultimate phalanx of the third to the base or middle of the antepenultimate phalanx of the fourth finger. The legs are long and slender; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends beyond the tip of the snout. A strong transverse dermal fold is present on the heel; the tarsal fold is weak to moderately developed and seldom extends the full length of the tarsus. The inner metatarsal tubercle is rounded, elliptical, and broadly visible from above. No outer metatarsal tubercle is evident. The toes are long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are moderately large and conical, and the supernumerary tubercles are moderately large and subconical. The toes are about three-fourths webbed (fig. 10SB). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. There is no noticeable anal sheath, but vertical dermal folds are present on either side of the anal opening and numerous small tubercles are present below the opening. The skin on the throat, belly, and posteroventral surfaces of

the thighs is strongly granular; elsewhere, the skin is smooth. The tongue is broadly cordiform, noticeably notched posteriorly, and barely free behind. The dentigerous processes of the prevomers form sharply angled, narrowly separated, long elevations between the moderately large, round choanae. Males have 10 to 12 teeth on each process and a total of 20 to 24 (mean, 22.3) prevomerine teeth; females have 12 to 14 teeth on each process and a total of 25 to 28 (mean, 26.4) prevomerine teeth. The vocal slits extend along the inner edge of the jaw from the midlateral base of the tongue to the angle of the jaw. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla crepitans* is pinkish tan with irregular brown markings and usually a dark brown middorsal line (pl. 50, fig. 2). At night the dorsum varies from yellowish tan to pinkish tan with darker brown irregular markings on the back and narrow transverse bars on the dorsal surfaces of the limbs. A narrow, dark brown line commences on the snout and extends posteriorly to about the sacral region. The flanks are creamy tan with numerous dark brown vertical bars. The anterior and posterior surfaces of the thighs are pale pinkish tan; narrow brown vertical bars are present on the posterior surfaces. The anal area is dark brown, and the tubercles below the anal opening are tipped with white. The webbing is pinkish tan. The chin is white with brown flecks; the chest is white, and the abdomen is pale orange. The iris is silvery bronze or pale creamy yellow with a silvery cast; in some individuals there is a faint greenish tint on the dorsal part of the iris. The palpebral membrane is unmarked.

By day, this frog becomes pale ashen gray; in some specimens there is no trace of dorsal markings, whereas in others the middorsal dark line is evident.

In preservative, the dorsum is pale tan to pale reddish brown with darker brown spots and irregular markings on the back and narrow transverse bands on the limbs. The vertical marks on the flanks and posterior surfaces of the thighs are dark brown or gray. The belly is creamy white.

TADPOLES: No tadpoles are available from Central America; the following description is

based on K.U. No. 110600 from Villavicencio, Departamento de Meta, Colombia. A tadpole in developmental stage 39 has a body length of 18.0 mm. and a total length of 54.5 mm. In dorsal profile the body is ovoid; it is slightly wider than deep. The snout is rounded in dorsal and lateral profiles. The eyes are moderately large, not widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point on the midline about two-thirds of the distance from the tip of the snout to the posterior end of the body. The caudal musculature is moderately heavy and tapers gradually to terminate just short of the pointed tip of the tail. The ventral fin is shallow, whereas the dorsal fin is much deeper and reaches a high point at about the midlength of the tail; at this point the depth of the dorsal fin is slightly greater than the depth of the caudal musculature. The dorsal fin does not extend onto the body (fig. 110A).

The dorsum and caudal musculature is pale yellowish tan; soft brown and gray suffusions are present on the dorsum of the body and caudal musculature and on the dorsal fin. In preservative, the body is pale gray with

scattered black flecks. The venter is white. The caudal musculature is creamy tan with faint gray blotches; the caudal fins are transparent with faint grayish brown flecks.

The mouth is anteroventral and small; its width is equal to about one-third of the greatest width of the body. The median part of the upper lip is bare; elsewhere, the lips are bordered by a single row of conical papillae. The lips are folded laterally. The beaks are relatively slender and bear fine serrations. The upper beak is transverse with posteriorly angled lateral processes that are slightly expanded distally. The lower beak is broadly V-shaped. There are two upper and four lower rows of teeth. The upper rows extend laterally to the margins of the lip and the second upper row is narrowly interrupted medially. The first and second lower rows are equal in length, but slightly shorter than the upper rows. The first lower row is narrowly interrupted medially. The third lower row is somewhat shorter than the first and second, and the fourth lower row is extremely short (fig. 111A).

MATING CALL: The call of *Hyla crepitans* consists of a quickly repeated series of short, poorly modulated notes. Although several recordings were obtained, most of these are not



FIG. 110. Tadpoles of the *Hyla boans* group. A. *Hyla crepitans*, K.U. No. 110600. $\times 2$. B. *Hyla rosenbergi*, A.M.N.H. No. 51791. $\times 4$. C. *Hyla boans*, K.U. No. 116777. $\times 2.5$.

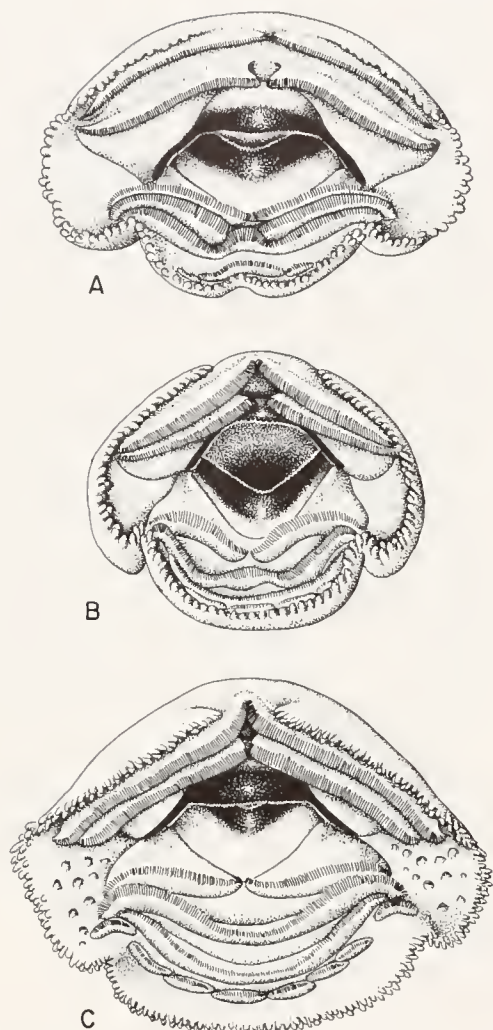


FIG. 111. Mouths of tadpoles of the *Hyla boans* group. A. *Hyla crepitans*, K.U. No. 110600. $\times 15$. B. *Hyla rosenbergi*, A.M.N.H. No. 51791. $\times 20$. C. *Hyla boans*, K.U. No. 116777. $\times 15$.

suitable for analysis, because of background noise from the call of *Physalaemus pustulosus* and *Leptodactylus*. Recordings of three individuals are suitable for analysis. In these, the call rate varies from 12 to 24 (mean, 22) call groups per minute. There are three to five notes in each call group. The duration of each note varies from 0.03 to 0.04 of a second, and there are approximately 110 pulses per second. The fundamental frequency varies from 178 to 185 (mean, 182) cycles per second and the dominant frequency varies from 965 to 1288 (mean, 1107) cycles per second (pl. 25, fig. 1).

NATURAL HISTORY: *Hyla crepitans* inhabits subhumid environments in lower Central America; apparently, its activity is limited to the rainy season, when the frogs congregate in shallow, grassy rainpools for breeding purposes. No evidence of a basin-like nest was observed by me or by Fouquette ("1966" [1967], p. 170) in Panamá. On June 18, 1963, at Camp Chagres, Canal Zone, Panamá, numerous calling males and three clasping pairs were found in shallow water in a flooded field. These observations agree with those of Stebbins and Hendrickson (1959, p. 520), who stated: "Both at Villavieja and Villavicencio [Colombia] and vicinity we found this frog [*Hyla crepitans*] in grassy areas with scattered bushes but not in the interior of dense forest. Several were found at the edge of riparian growth. The animals were usually found in or near the water of quieter parts of the streams or temporary rainpools." The same authors (1959, p. 522) mentioned eggs of this species. "The female was later opened, and a total of 1,064 eggs, ready for laying, were removed from her oviducts. At Villavicencio on November 19, 1950, two pairs in amplexus were found in the water at the edge of rainpools. Two days later, upon removing them from a container in which they had been kept alive, we found the females had deposited eggs. These were surrounded by two jelly layers, the outer one adherent, the eggs forming a loose cluster. In alcohol, the diameters of the ova are 1.3 to 1.5 mm. and, of the outer jelly layer, 3.5 to 4.4 mm." Dr. John Lynch obtained the tadpoles of this species from rainpools in a grassy field at Villavicencio on July 5, 1967.

REMARKS: *Hyla levillantii*, *doumercii*, and *xerophilla* Duméril and Bibron (1841) and *Hyla indris* Cope (1867a) are usually placed in the synonymy of *Hyla crepitans*. *Hyla xerophilla* was named from Cayenne, whereas the other three species were named from Surinam. The variability displayed by *Hyla crepitans* in South America suggests the possibility that geographical races possibly are recognizable; perhaps, more than one species is involved. Consequently, because none of these names is based on Central American material, I have not included them in the synonymy. Cochran (1955) included *Hyposiboas circumdatus* Cope

(1867a) in the synonymy of *Hyla crepitans*. Werner C. A. Bokermann has informed me (*in litt.*) that this Brazilian frog as now recognized probably consists of a complex of several species.

The status of *Hyla pugnax* Schmidt (1857) possibly is open to question. The type specimen can not be located; on the basis of the type description, it is highly possible that *pugnax* is the same as *crepitans*, although the possibility exists that it might be *Hyla rosenbergi*. However, on the basis of size (62 mm.) as given by Schmidt and on the reduced amount of webbing between the third and fourth fingers, it is most likely that this name is associated with the frog now known as *Hyla crepitans*.

Lynch and Fugler (1965, p. 11) recorded *Hyla crepitans* from "Laguna Yogoá," Departamento de Cortez, Honduras. This record was based on a single male, A.M.N.H. No. 45997 (in the Pratt collection from Honduras). According to the catalogues in the American Museum of Natural History, the specimen came from Tela, not Lago Yogoá. This speci-

men is the only individual of *Hyla crepitans* known from north of Panamá. I would be highly skeptical of the record if it were not for the presence in the same area of *Cnemidophorus lemniscatus*, another species unknown in Central America between central Panamá and northern Honduras [see Echternacht (1968)].

ETYMOLOGY: The specific name is Latin, meaning rattling, and evidently refers to the rattle-like call of this species.

DISTRIBUTION: *Hyla crepitans* occurs in subhumid environments on the Pacific lowlands of central Panamá and the Caribbean lowlands of northern Honduras (fig. 112); the species is widely distributed in South America east of the Andes.

See Appendix 1 for the locality records of the 77 specimens examined.

Hyla rosenbergi Boulenger

Hyla rosenbergi Boulenger, 1898a, p. 123 [syntypes, B.M.N.H. Nos. 1947.2.12.71-75 from Cachabe, Esmeraldas Province, Ecuador; W. F. H. Rosenberg collector]. Taylor, 1954b, p. 626.

DIAGNOSIS: This large frog has a mottled

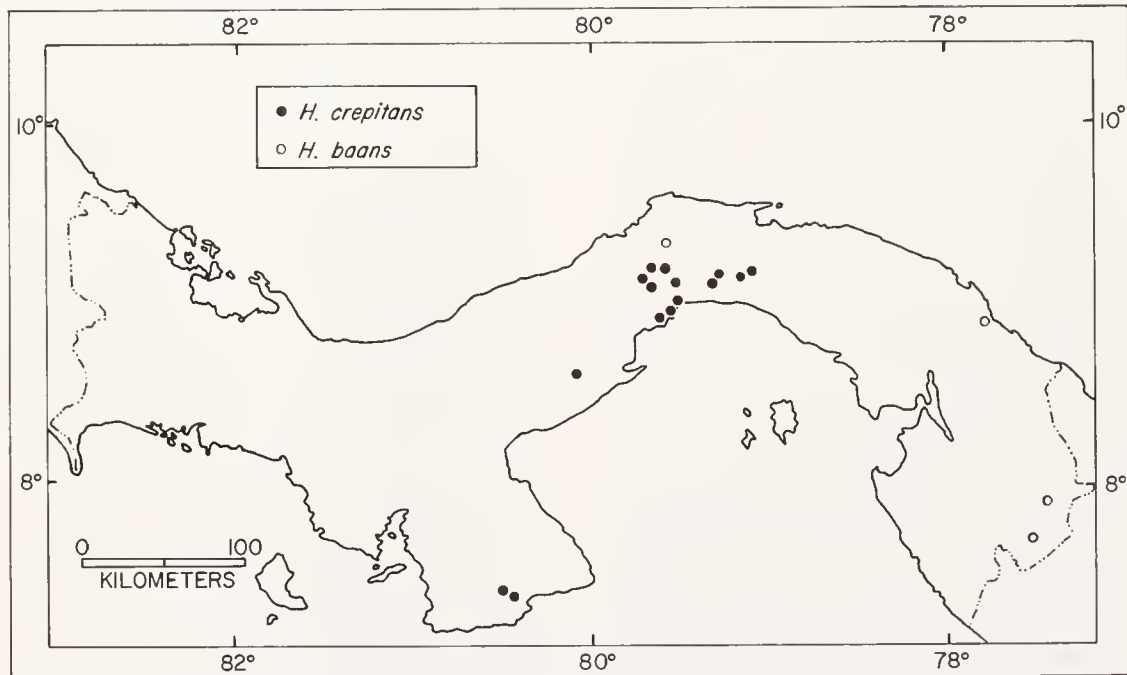


FIG. 112. Distribution of *Hyla crepitans* and *Hyla baans*. A record for *H. crepitans* from Tela, Honduras, is not shown.

dorsum, vertical dark lines on the flanks and posterior surfaces of the thighs, a long, low snout, and a protruding prepollex. It differs from *Hyla crepitans* by having more webbing; the web extends to the base of the disc on the fourth finger in *rosenbergi* but only to the distal end of the antepenultimate phalanx in *crepitans*. Furthermore, *rosenbergi* is a much larger species (males to 90 mm., as compared to 58 mm. in *crepitans*). *Hyla rosenbergi* differs from *boans* by lacking a calcar on the heel and reticulations on the palpebral membrane and by having pale, instead of dark, webbing. The smaller *Hyla rufitela* can be distinguished by having less webbing (red in life), a green dorsum, and unmarked flanks and thighs. Frogs of the *Hyla miliaria* group and *Plectrohyla* also have projecting prepollices. Frogs in the former group have fully webbed hands and feet and dermal fringes on the limbs. Frogs in the genus *Plectrohyla* have robust bodies and arms, short snouts, and long fingers with small discs and little webbing.

DESCRIPTION: Males of this large species attain a maximum snout-vent length of 90.0 mm., and females reach 93.2 mm. In a series of 18 males from the Río Tuira at the Río Mono, Darién Province, Panamá, the snout-vent length is 78.0 to 85.3 (mean, 82.1) mm.; the ratio of tibia length to snout-vent length is 0.535 to 0.593 (mean, 0.565); the ratio of foot length to snout-vent length is 0.407 to 0.435 (mean, 0.424); the ratio of head length to snout-vent length is 0.319 to 0.349 (mean, 0.333); the ratio of head width to snout-vent length is 0.312 to 0.327 (mean, 0.321), and the ratio of the diameter of the tympanum to that of the eye is 0.797 to 0.972 (mean, 0.878). Seven females from the same locality have snout-vent lengths of 82.6 to 90.8 mm. and do not differ significantly in proportions from the males. Panamanian specimens agree with those from the vicinity of the type locality in Esmeraldas Province, Ecuador; 24 males from Esmeraldas have snout-vent lengths of 77.7 to 90.8 (mean, 83.6) mm. Specimens from the western part of the range in Puntarenas Province, Costa Rica, are noticeably smaller; 15 males have snout-vent lengths of 63.0 to 75.7 (mean, 67.9) mm.

The head is nearly as wide as the body,

and the top of the head is slightly concave. In dorsal profile, the snout is acutely rounded; and in lateral profile, it is bluntly rounded. The snout is long; the protuberant nostrils are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is slightly elevated and rounded; the loreal region is inclined ventrolaterally, and the lips are thin and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to less than half of the diameter of the tympanum.

The upper arms are slender, whereas the forearms are moderately robust. An axillary membrane is absent. A distinct glandular ridge extends from the elbow on to the base of the fourth finger, and a weak transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear large discs; the width of the disc on the third finger is equal to about three-fourths of the diameter of the tympanum. The subarticular tubercles are large and flattened; none is bifid. The supernumerary tubercles are small, subconical, and indistinct. A low, flat, partially bifid palmar tubercle is present. In males, the prepollex is greatly enlarged and projecting; in some individuals, the prepollical spine protrudes through the skin of the prepollex. The fingers are about three-fourths webbed (fig. 109A). The webbing extends from the distal end of the antepenultimate phalanx of the first finger to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, and from the middle of the penultimate phalanx of the third to the distal end of the penultimate phalanx of the fourth finger. The hind limbs are moderately long, but not especially slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibio-tarsal articulation extends to a point between the eye and the nostril. A transverse dermal fold is present on the heel, and several small tubercles are evident on the heel. A distinct, curved, inner tarsal fold extends the full

length of the tarsus, and a distinct, straight outer tarsal fold also is present. The inner metatarsal tubercle is low, flat, elliptical, and barely visible from above. In some individuals, a faint outer metatarsal tubercle is evident. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are small, conical, and present only on the proximal segments of each digit. The toes are about four-fifths webbed (fig. 109C). The webbing extends from the base of the disc of the first toe to the base of the disc of the second and on to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs and is covered by a short anal sheath. Numerous small tubercles and a pair of vertical dermal folds are present below the anal opening. The skin on the throat, belly, and posteroventral surfaces of the thighs is granular; elsewhere, the skin is smooth, except that in many individuals, minute tubercles are present on the dorsum, especially on the head. The tongue is elongately ovoid, emarginate, or very shallowly notched posteriorly and not free behind. The dentigerous processes of the prevomers are strongly angled, narrowly separated elevations between the large, quadrangular choanae. Males have 14 to 17 teeth on each process and a total of 29 to 33 (mean, 31.0) prevomerine teeth, whereas females have 16 to 18 teeth on each process, and a total of 32 to 35 (mean, 33.8) prevomerine teeth. The vocal slits extend along the inner edge of the jaw from the anterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Hyla rosenbergi* consists of a yellowish tan dorsum with or without faint mottling and usually with a distinct dark brown middorsal line (pl. 50, fig. 4). The dorsum varies from pale yellowish tan to reddish tan or olive-gray, usually with faint, irregular darker blotches. Most

individuals have a dark brown or black mid-dorsal line beginning on the snout and extending to the scapular or even to the sacral region. The flanks and posterior surfaces of the thighs are pale yellowish brown with creamy gray vertical bars, which usually are wider than the paler interspaces. The anterior surfaces of the thighs and the webbing varies from yellowish tan to pale orange-brown. The throat is yellowish gray, and the belly is pale bluish green. The blue is most intense in the axilla and proximally on the ventral surfaces of the thighs. The iris is pale golden above and silvery white below.

In preservative, the dorsum varies from reddish brown to pale creamy tan; indistinct and irregular darker transverse bars are evident on the dorsal surfaces of the limbs in some individuals. The markings on the posterior surfaces of the thighs usually are evident; in some individuals these markings consist of rather narrow, vertical dark lines, whereas in others, the interspaces are much narrower than the broad vertical dark marks. The markings on the flanks basically consist of a series of vertical dark lines, but in many individuals these are interconnected, so as to form a network. In most breeding males, the throat is dark gray or grayish brown, with or without creamy white flecks; however, the throat in some males is creamy white with a faint suffusion of gray.

TADPOLES: I have not obtained the tadpoles of this species in Central America; the following description is based on A.M.N.H. No. 51791 from Camp Creek, below Yavisa, Darién Province, Panamá (Breder, 1946, p. 409). A tadpole in developmental stage 27 has a body length of 9.2 mm. and a total length of 27.0 mm. The body is ovoid in dorsal profile and has a rounded snout; in lateral profile, the snout is acutely rounded; the eyes are moderately large, broadly separated and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point on the midline slightly posterior to the midlength of the body. The anal tube is moderately short and dextral. The caudal musculature is moderately robust and tapers gradually to a slender point at the

tip of the pointed tail. The ventral fin is shallow anteriorly and somewhat deeper posteriorly, whereas the dorsal fin is much deeper than the ventral one and does not extend on to the body (fig. 110B).

In preservative, the dorsum of the body is dark brown, and the venter is creamy tan. The caudal musculature is pale brown; dark brown flecks and blotches are present on the caudal musculature and fins. The pigment tends to form transverse bars on the dorsal surface of the musculature.

The mouth is anteroventral and small; the width of the mouth is equal to about one-third of the greatest width of the body. The mouth is completely bordered by papillae; medially on the upper lip there is only one row, but for the most part two rows are present on the rest of the lips, which are deeply folded laterally. The beaks are moderately slender and bear pointed serrations. The upper beak is broad and has long slender lateral processes. The lower beak is broadly V-shaped. There are two upper and four lower rows of teeth. The upper rows are long and extend to the margins of the lips; the second upper row is narrowly interrupted medially. The first lower row is interrupted medially in some specimens. The first three lower rows are nearly as long as the upper ones, whereas the fourth lower row is noticeably shorter and fragmented in some individuals (fig. 111B).

Breder (1946, pp. 414-415) illustrated the development of *Hyla rosenbergi* based on the tadpoles that I have examined. His otherwise excellent series of illustrations is marred by an error of not showing the fourth lower tooth row in the mouth of *Hyla rosenbergi*.

MATING CALL: The call of *Hyla rosenbergi* consists of a short series of low-pitched short notes, "tonk-tonk-tonk." The call is loud and carries for great distances. Recordings obtained in Costa Rica were compared with those from eastern Panamá and found not to differ significantly. Call groups consist of two to five (mean, 2.8) notes. Call groups are repeated at a rate of 32 to 58 (mean, 43) groups per minute. Each note has a duration of 0.05 to 0.07 (mean, 0.06) of a second. The fundamental frequency varies from 130 to 143 (mean, 136) cycles per second. The second harmonic is the dominant frequency at 260

to 286 (mean, 272) cycles per second (pl. 25, fig. 3).

NATURAL HISTORY: *Hyla rosenbergi* is a forest inhabitant. The breeding season seems to be rather long in this species. Calling males have been heard from April through August in southeastern Costa Rica.

Although I have never observed mating in this species, I have encountered numerous calling males. At Tacarcuna and the Río Mono in Darién Province, Panamá, males were calling from trees over swamps. At the latter locality, and at several sites in Puntarenas Province, Costa Rica, I have observed the males calling from shallow water in swamp forest or in marshes. However, I have not observed clasping pairs or the deposition of eggs. My own observations seem to be in contradiction with the detailed report on the life history of this species by Breder (1946, pp. 409-416, pls. 48-53). However, I reiterate that I have not observed actual mating; probably my observations are indicative only of the calling behavior early in the breeding season.

Breder presented a detailed account of the mating behavior in *Hyla rosenbergi*; his observations were made at Camp Creek, below Yavisa, Darién Province, Panamá, in March 1924. He stated: "Breeding is accomplished in the heavy forest along the banks of drying stream beds. Here the male makes a circular depression, typically in the soft earth at the edges of the remaining pools. These fill with water, usually by seepage, and here the males sit and call . . . although during the nest constructing, frogs are very timid, in strong contrast to their later behavior, the normal nests are evidently made by the males' pivoting around on their hind end and patting the walls with their front feet." Breder gave measurements for 16 nests, which had diameters of 20 to 33 (mean, 27.0) cm. and depths of 13 to 82 (mean, 51) mm. Breder commented that after the nest was constructed, the males called repeatedly for several nights until females were induced to mate with them.

Breder (1946, p. 413) noted that the males remained in the nests and the females come to the nests, apparently attracted by the calling of the male. Breder illustrated by a series

of photographs a sequence in which the male left the nest. He stated: "It was the only time in which a male was noted to leave his nest and pursue a female that evidently was not about to enter. It is evident that the female entered the back of the nest, that is, at the side to which the male had his back. Other observations indicate that this is the usual order of procedure. It allows the female to jump on the back of the male, which may not be necessary but is usually done. The male at once turns and reverses the position as shown in the final photograph in that series. As earlier noted, the placing of another male near the nest caused the owner to face the other way. It is possible, although it could not be determined in the field, that actually the male is presenting his back to a possible female visitor as part of the courtship procedure."

Goeldi (1895, p. 89) first reported the building of such kinds of nests in *Hyla faber*; as pointed out by Lutz (1960, p. 61) Goeldi erroneously thought that the females built the nests. However, in *Hyla faber*, like in *rosenbergi*, the males do the construction. Lutz also presented observations on aggressive behavior between males of *Hyla faber* and pointed out that the fighting males utilize the long curved prepollical spines.

Breder's tadpoles were obtained in March. In the same month, he also obtained several metamorphosing young. Five completely metamorphosed young have snout-vent lengths of 13.8 to 15.5 (mean, 14.8) mm. The small frogs have faint transverse bands on the limbs and practically no webbing between the fingers.

REMARKS: On June 1, 1962, Richard E. Zweifel collected a single specimen of a *rosenbergi*-like *Hyla* (A.M.N.H. No. 69766) from the Río Bejuco, near Bejuco, Panamá Province, Panamá. This specimen, an adult male having a snout-vent length of 78.2 mm. lacks a mid-dorsal dark stripe and has reduced webbing between the fingers; in the latter character it is much like *Hyla crepitans*. Zweifel collected this specimen as a voucher for an uncollected tape-recorded specimen. The recording (A.M.N.H. Tape No. 122-2; pl. 25, fig. 2) of the other individual, one of several not collected, is difficult to place; in certain aspects

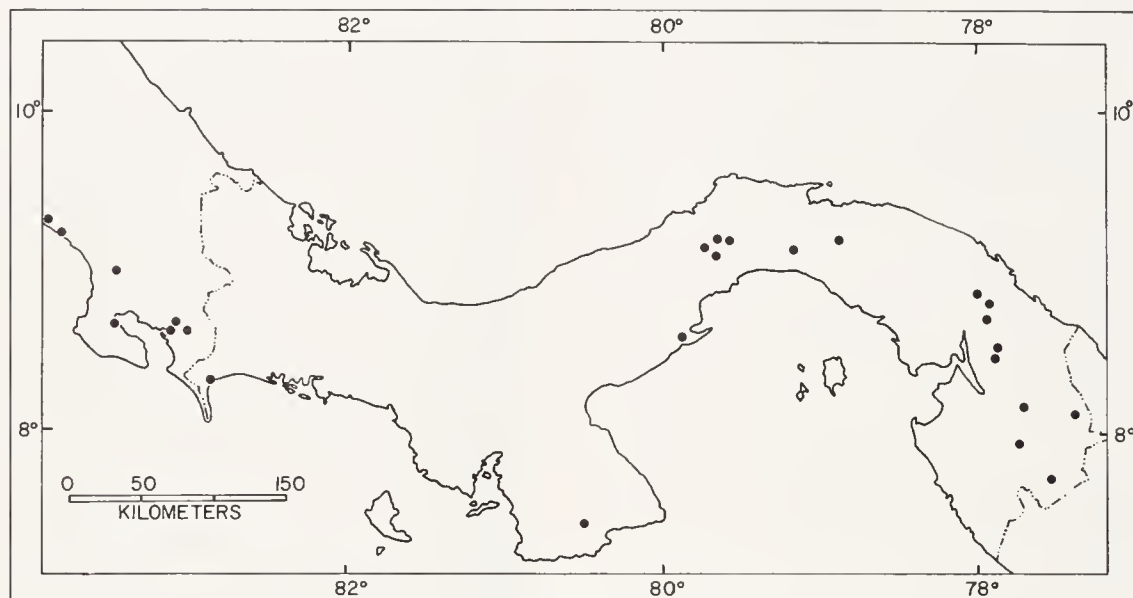
it is like *crepitans* and in others like *rosenbergi*. The call is a continuous series of notes; the repetition rate is 130 notes per minute. Each note has a duration of 0.08 of a second. The fundamental frequency is 135 cycles per second, and two harmonics (405 and 1215 cycles per second) are emphasized. Perhaps, at this locality, there is a population of hybrids between *Hyla crepitans* and *Hyla rosenbergi*.

Noble (1924, p. 66) first recorded *Hyla rosenbergi* from Central America. Apparently the first Panamanian specimen was collected on the Río Bayano on March 22, 1911, by Meek and Hildebrand. The second individual (U.S.N.M. No. 50209) supposedly was obtained on June 6, 1912, by E. A. Goldman at Cana, Darién Province, Panamá (Schmidt, 1933a, p. 6). The record from Cana is questionable; *Hyla rosenbergi* occurs only at low elevations, and Cana lies at an elevation of 500 meters. Perhaps, the specimen came from the Tuira Valley adjacent to the Serranía de Pirre where Cana is located, or maybe this is the specimen that Noble (1924, p. 6) reported from Arrijam (=Arraijan). Netting (1935, p. 15) reported the species from the Canal Zone and noted that the two specimens from there did not agree perfectly with the description and figure of an Ecuadorian specimen given by Boulenger (1898a, p. 123). A comparison of the series of specimens now available from Costa Rica and Panamá with a recently obtained series of 28 specimens from Esmeraldas Province, Ecuador, shows no noticeable differences, except that specimens from the southern part of the range are somewhat larger than those from the northern part.

Hyla rosenbergi seems to occupy an ecological position intermediate between *Hyla crepitans* and *boans*. The latter seemingly is restricted to more humid forest, whereas the former is an inhabitant of drier forest. In the northeastern part of the range, in Puntarenas Province, Costa Rica, *Hyla rosenbergi* seems to be restricted ecologically by the dry forest, because in that part of the range the species only inhabits the humid forest of the Golfo Dulce region.

ETYMOLOGY: The specific name is a patronym for Mr. W. F. H. Rosenberg, the collector of the type specimen.

DISTRIBUTION: *Hyla rosenbergi* is known

FIG. 113. Distribution of *Hyla rosenbergi*.

from the Pacific lowlands of lower Central America and northwestern South America; it ranges from extreme southeastern Costa Rica, through Panamá and Colombia to northwestern Ecuador (fig. 113).

See Appendix 1 for the locality records of the 190 specimens examined.

Hyla boans (Linnaeus)

Rana boans Linnaeus, 1758, p. 213 [no type designated; from "America"; Andersson (1900, p. 17) noted a type specimen without a number in the Royal Museum of Sweden].

Rana maxima Laurenti, 1768, p. 32 [based on Seba (1734, pl. 72, fig. 3); no locality designated].

Hyla boans: Daudin, 1803, p. 64. Andersson, 1900, p. 17.

Calamita maxima: Schneider, 1799, p. 163.

Hyla maxima: Günther, 1859, p. 99.

DIAGNOSIS: This large species has a mottled dorsum, dark posterior surfaces of the thighs, a long, low snout, and a protruding prepollex. It differs from other Central American species in the group by having a calcar on the heel, nearly fully webbed hands and feet, a reticulated palpebral membrane, and dark webbing. *Hyla rosenbergi* and *crepitans* have vertical dark lines on the posterior surfaces of the thighs and pale webbing; both

species lack a calcar and reticulations on the palpebral membrane. *Hyla rufitela* also lacks a calcar and reticulations on the palpebral membrane; furthermore, this smaller species has less webbing (red in life) and a green dorsum. The members of the *Hyla miliaria* group and *Plectrohyla* also have projecting prepollices; the former group differs from *Hyla boans* by having dermal fringes on the limbs, and frogs in the genus *Plectrohyla* have more robust bodies, shorter heads, more robust arms, and proportionately longer fingers with much smaller discs and less webbing.

DESCRIPTION: This is the largest hyloid frog in Middle America; males attain a snout-vent length of 132 mm., and females are known to reach 117.5 mm. In a series of 10 males from Camp Sasardí, San Blas, Panamá, the snout-vent length is 100.7 to 131.9 (mean, 119.9) mm.; the ratio of tibia length to snout-vent length is 0.493 to 0.555 (mean, 0.517); the ratio of foot length to snout-vent length is 0.424 to 0.457 (mean, 0.436); the ratio of head length to snout-vent length is 0.337 to 0.362 (mean, 0.347); the ratio of head width to snout-vent length is 0.340 to 0.369 (mean, 0.352), and the ratio of the diameter of the tympanum to that of the eye is 0.569 to 0.649 (mean, 0.614). Two adult females from the same locality have snout-vent lengths of 116.3

and 117.5 mm.; they do not differ significantly from the males in proportions.

The head is nearly as wide as the body, and the top of the head is noticeably concave. The eyes are moderately prominent and widely separated. In dorsal profile the snout is acutely rounded; in lateral profile it is round. The snout is extremely long, nearly twice as long as the orbit. The nostrils are noticeably protuberant at a point about five-sixths of the distance from the eyes to the tip of the snout. The canthus is elevated and rounded; the loreal region is barely concave and slopes outward to the thin, barely flared lips. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point just posterior to the angles of the jaws. The fold obscures the upper edge of the tympanum, which otherwise is distinct, separated from the eye by a distance slightly less than the diameter of the tympanum, and directed dorsolaterally.

The arms are moderately long and robust; an axillary membrane is absent. A low tubercular fold is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear large discs; the width of the disc on the third finger is half again the diameter of the tympanum. The subarticular tubercles are large and subconical; none is bifid. The supernumerary tubercles are indistinct or absent. No distinctive palmar tubercle is evident. In males, the prepollex is greatly enlarged and projecting; in some individuals, the tip of the prepollical spine protrudes through the end of the prepollical process. The fingers are about three-fourths webbed (fig. 109B). The webbing extends from the distal end of the antepenultimate phalanx of the first finger to the distal end of the antepenultimate phalanx of the second; from the base of the disc of the second to the base of the penultimate phalanx of the third, and from the base of the disc of the third to the base of the disc of the fourth finger. The hind limbs are moderately long and robust. The heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the tip of the snout. A transverse dermal fold and a small triangular dermal flap, or calcar, are present on the heel. An

elevated, curved, inner tarsal fold is present. A weak, straight, outer tarsal fold is evident in some individuals. The inner metatarsal tubercle is large, flattened, and elliptical. No outer metatarsal tubercle is present. The toes are long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately large and subconical; supernumerary tubercles are absent. The toes are fully webbed (fig. 109D).

The anal opening is directed posteriorly at the upper level of the thighs. The opening is bordered below by numerous small tubercles. The skin on the throat, belly, and ventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is elongately ovoid, usually widest posteriorly, not free behind and usually emarginate. The denticulous processes of the prevomers are narrowly separated or in contact medially. The processes are strongly angular (transverse anteromedially and inclined posterolaterally). The posterolateral projections of the processes form the postero-median border of the large, quadrangular choanae. Males have 19 to 29 teeth on each process and a total of 39 to 53 (mean, 48.3) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Hyla boans* consists of a grayish brown or an orange-brown dorsum with darker brown irregular mottling on the body and transverse bands on the lips (pl. 51, fig. 1). Some individuals are pale reddish tan or orange-brown (pl. 51, fig. 2). The throat is dark gray, the chest, belly, and ventral surfaces of the thighs are yellowish white. There is a slight bluish tint to the digital pads and to the undersides of the limbs and throat. The flanks are mottled with dark brown. The posterior surfaces of the thighs are dark brown or dark gray. The palpebral membrane is reticulated with silver.

In preservative, the dorsum is dull brown or dull gray with darker brown blotches and reticulations on the back, and transverse bands on the limbs; in some individuals the dorsum is pale pinkish tan with faintly darker markings on the body and dorsal surfaces of the

limbs. In some individuals a narrow brown middorsal stripe begins on the snout and extends posteriorly on the body. The posterior surface of the thighs are dull brown or gray, usually without any evident pattern, but in some of the paler colored specimens, the transverse bands on the dorsal surfaces are continuous onto the posterior surfaces of the thighs. The webbing on the hands and feet is dark brown, dark gray, or black. The throat is gray in all males.

Recently metamorphosed young are pale brown above with black dots; the palpebral reticulation is absent. Two individuals having snout-vent lengths of 32.0 mm. show an intermediate phase of coloration. The dorsal surfaces of the body and limbs are pale orange-brown with darker brown bands on the limbs. The body is punctated with black. The posterior surfaces of the thighs are gray, and the flanks are reticulated with white and dark gray (pl. 50, fig. 3). The iris is pale brown with an orange-brown horizontal streak through the pupil, and the palpebral membrane is reticulated with pale yellowish brown.

TADPOLES: Tadpoles of this species are available from Camp Sasardí, San Blas, Panamá, and from Santa Cecilia, Napo Province, Ecuador; a typical tadpole in developmental stage 36 from the former locality has a body length of 14.5 mm. and a total length of 40.0 mm. The body is ovoid, widest posteriorly, and noticeably wider than deep. In dorsal profile the snout is bluntly rounded, and in lateral profile it is acutely rounded. The eyes are moderately small, not widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point just below the midline about two-thirds of the distance from the snout to the posterior end of the body. The anal tube is short and dextral. The caudal musculature is moderately slender and tapers to a point just proximal to the tip of the pointed fin. The ventral fin is shallow throughout its length, whereas the dorsal fin, which does not extend onto the body, is deepest at about midlength of the tail, at which point it is noticeably deeper than the caudal musculature (fig. 110C).

The body is pale brown with dark green mottling. In preservative, the dorsum of the body is mottled dark brown and creamy tan; the venter is pale bluish white. The caudal musculature is pale creamy tan with dark brown blotches and reticulations; the latter extend onto the fins. The blotches tend to form transverse bands across the dorsal part of the caudal musculature.

The mouth is anteroventral and moderately small; its width is equal to not more than half of the greatest width of the body. The median part of the upper lip is bare; the rest of the lips are bordered by a single row of moderately large, subconical papillae. Deep lateral folds are present in the lips. The beaks are moderately well developed and bear short serrations. The upper beak is broad and nearly uniform in depth; long slender, terminally expanded, lateral processes are present. The lower beak is broadly V-shaped. There are two upper and four lower rows of teeth. The upper rows are long, and the second upper row is narrowly interrupted medially. The first three lower rows are equal in length, but shorter than the upper ones. The fourth lower row is noticeably shorter (fig. 111C).

Hatchling tadpoles have a total length of about 4.5 mm. Large, filamentous gills and prominent oral suckers are present; the yolk sac is still large. The cornea is not transparent upon hatching. The hatchlings are dark brown or black in color.

MATING CALL: The call of *Hyla boans* consists of a series of short, low-pitched notes. Usually each call group consists of three to 10 notes, although one individual produced 41 consecutive notes. The note repetition rate varies in three recordings from Camp Sasardí, Panamá, from 44 to 82 (mean, 69) notes per minute. The notes have a duration of 0.25 to 0.28 (mean, 0.26) of a second and a pulse rate of 100 to 120 (mean, 107) pulses per second. The fundamental frequency varies from 104 to 130 (mean, 114) cycles per second, and the dominant frequency varies from 832 to 910 (mean, 869) cycles per second (pl. 20, fig. 3).

NATURAL HISTORY: *Hyla boans* inhabits humid tropical forest. Observations of this species in Central America are extremely limited. Two juveniles were obtained from a bush and a tree in Darién Province in July,

1965. Charles W. Myers obtained some interesting data on the calling and breeding behavior of the species at Camp Sasardí, San Blas Province, Panamá, in January and February, 1967. Between January 11 and 13, he observed 10 males calling from trees along a river. Some of the individuals were at least 7 meters above the ground. On February 4, he found a male and a gravid female perched side by side on the limb of a tree, and on February 8, he found a male and female side by side in a freshly constructed nest.

The following description of the nest is taken from the field notes of Charles W. Myers for February 8, 1967: "Since there are considerable differences in the sizes of tadpoles in some nests and because I noticed some tadpoles in a nest where eggs had just been laid, the same nest seems sometimes to be used more than once. The nests are circular and made at the edge of a sand or gravel bar or on tiny flats that result from deposition of sediment in the creek mouths . . . because the water level may vary from day to day, depth measurements were taken only from two fresh nests (*i.e.*, containing eggs), both in sand and fine gravel. A basin 31 cm. in diameter was 6 cm. deep (bottom to water surface) in the center, and one 40 cm. in diameter was 7 cm. deep. One nest contained 2,722 eggs, but I saw another nest containing what seemed to be twice this number of hatchlings."

Myers observed that two nests were built from coarse gravel, five nests from sand, and 15 nests in sand and fine gravel (pl. 9). The diameters of the 22 nests vary from 28 to 51 (mean, 36.5) cm.

The breeding season may be rather extended in this species, because in early February, Myers found at Sasardí gravid females, nests containing eggs, tadpoles in all stages of development, and recently metamorphosed young. Two recently metamorphosed young have snout-vent lengths of 16.6 and 17.5 mm.

REMARKS: For many years, this large tree frog was known by the name *Hyla maxima* (Laurenti, 1768). The earlier name for this species, *Hyla boans* (Linnaeus, 1758) had been overlooked until 1900 when the name was resurrected by Andersson (1900, p. 17). Although *boans* Linnaeus, 1758, has priority over *maxima* Laurenti, 1768, the name *max-*

ima was used widely for many years between 1850 and 1950. Goin and Layne (1958, p. 111) argued that on the basis of the Copenhagen Decisions (Hemming, 1953, p. 25) it would be better to retain the name *maxima* for the frogs known so long under that name than to use the name *boans* Linnaeus, 1758, a *nomen oblitum*, pending the precise wording in the revised Code. Although the Code of Zoological Nomenclature (Stoll, 1961, Art. 23, b) provides for a *nomen oblitum* ruling in cases such as that involving *boans* and *maxima*, the rule has been indefinitely suspended. Therefore, it seems only reasonable to proceed under a strict adherence to the law of priority and utilize the name *boans* for this large and widespread species of frogs.

Several names apply to South American populations of this frog which apparently are synonyms of *Hyla boans*. However, due to some amount of uncertainty regarding the application of these names, and because none is based on Central American material, I have not included them in the synonymy. Most authors consider *Hyla zebra* (Shaw, 1802) and *Hyla palmata* Daudin, 1803, to be synonyms of *Hyla boans*. According to Cochran and Goin (1970), *Hyla lactea* Lönnberg, *Hyla wavrini* Parker, and *Hyla miranda-ribeiri* Melin are synonyms of *Hyla boans*.

ETYMOLOGY: The specific name *boans* is derived from the Greek Boanergēs, the sons of Thunder; the name apparently refers to the voice of the frog.

DISTRIBUTION: *Hyla boans* is widespread in tropical lowland forests in South America east of the Andes; the species also occurs in the Atrato Valley in northwestern Colombia and in eastern Panamá (fig. 112).

See Appendix 1 for the locality records of the 32 specimens examined.

The *Hyla pseudopuma* Group

DEFINITION: Members of this group are medium-sized pond-breeding species; males attain a maximum snout-vent length of 42.9 mm. and females, 47.6 mm. The dorsum is usually dull brown, marked by blotches, dorsolateral white stripes, or not. Transverse bands or dark flecks are present on the limbs. The iris is deep bronze, and the palpebral membrane is clear. The hands are no more

than one-third, and the feet two-thirds webbed. A distinct tarsal fold is present, but an axillary membrane and dermal folds or appendages on the limbs are absent. Males have a single, median, subgular or weakly bilobed vocal sac and horny nuptial excrescences on the prepollices. The skull is well ossified, and a moderately small frontoparietal fontanelle is present (fig. 114). The sphenethmoid is broad and extends anteriorly between the rather slender nasals, which are separated medially and broadly sutured to the sphenethmoid and have well-developed maxillary processes. The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosal extends about one-half of the distance to the maxillary. The quadratojugal is present and articulates with the maxillary. The prevomer is well ossified and bears teeth, and the medial ramus of the pterygoid is in bony contact with the prootic. The tadpoles have rather robust bodies, moderately deep fins, and anteroventral mouths with two upper and three lower rows of teeth. The mating calls consist of a series of moderately short, poorly modulated notes. The hap-

loid number of chromosomes is 12 (known only in *pseudopuma*).

COMPOSITION: Two species (*Hyla angustilineata* and *pseudopuma*), the latter with two subspecies, comprise this group, which is endemic to the highlands of Costa Rica and western Panamá. I have examined 489 preserved frogs, 24 skeletons, 40 lots of tadpoles, and one preserved clutch of eggs of the three taxa.

COMMENTS: The members of the *Hyla pseudopuma* group are unique in lower Central America by being upland pond-breeders. This breeding behavior, coupled with the similarities in cranial and larval structure are the basis for placing the species in a single group. The coloration of the two species is noticeably different.

Possibly the species differentiated from one another in two partially separated highland areas—*angustilineata* in the Cordillera Central north of the Mesa Central in Costa Rica and *pseudopuma* in the Cordillera Talamanca southeast of the Mesa Central. If such were the case, *pseudopuma* subsequently invaded the Cordillera Central, where it now occurs sympatrically with *angustilineata*.

The members of this group are generalized in their cranial structure, tadpoles, external characters, and mating behavior. Possibly, they represent virtually unmodified descendants from an early generalized hyliid stock in lower Central America.

Hyla pseudopuma Günther

Hyla pseudopuma Günther, 1901 (1885-1902), p. 274.

DIAGNOSIS: This moderate-sized brown *Hyla* with the fingers about one-third webbed is characterized by numerous pigmented supernumerary tubercles on the toes and yellow spots on dark brown or blue flanks. It differs from *Smilisca puma* by having a more acuminate snout and more webbing between the fingers. *Smilisca sordida* superficially resembles *Hyla pseudopuma* but has more webbing and many distinct pale blue or cream flecks on the posterior surfaces of the thighs, which are red, tan, or dark brown, unmarked, or with a few diffuse cream spots in *pseudopuma*.

CONTENT: Two subspecies are recognized: *Hyla p. pseudopuma* in the highlands of Costa

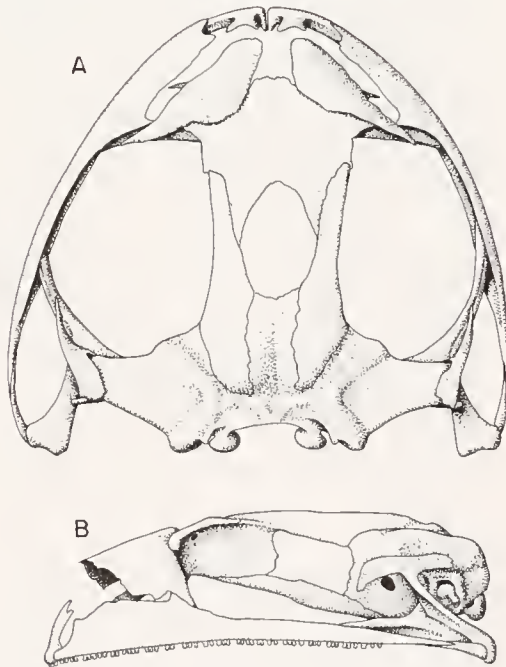


FIG. 114. Dorsal (A) and lateral (B) views of the skull of *Hyla pseudopuma*, K.U. No. 104347. $\times 5$.

TABLE 28

Comparison of Certain Measurements and Proportions, with Means in Parentheses, in Males of the Subspecies of *Hyla pseudopuma*.

Subspecies	N	Snout-vent Length	Tibia Length/ S-V L	Tympanum/ Eye
<i>pseudopuma</i>	30	37.6-41.4 (39.7)	0.485-0.550 (0.515)	0.476-0.667 (0.576)
<i>infucata</i>	30	37.6-42.9 (39.5)	0.504-0.569 (0.534)	0.432-0.568 (0.492)

Rica and Pacific slopes of western Panamá and *H. p. infucata* on the Atlantic slopes of western Panamá.

Minor differences exist in proportions (table 28), but the major structural difference between the subspecies is in the shape of the snout, which is bluntly rounded in lateral profile and acuminate in dorsal profile in *infucata* and acutely rounded in lateral profile and acuminate in dorsal profile in *pseudopuma* (fig. 115). The shape of the snout is dependent upon the nature of the underlying premaxillaries. In *infucata*, the premaxillaries lie in a transverse plane and have short, nearly vertical alary processes, whereas in *pseudopuma*, the premaxillaries lie at a slight angle and have longer alary processes that are inclined posteriorly.

The dorsal color and pattern is highly variable and subject to extreme metachrosis

in both subspecies. Nonetheless, the most obvious difference between the subspecies is in color. *Hyla p. infucata* has bright red flash colors on the thighs and webbing, whereas these surfaces in the nominate subspecies are tan or brown.

DISTRIBUTION: *Hyla pseudopuma* occurs at moderate to high elevations in the highlands of Costa Rica and western Panamá (fig. 116).

Hyla pseudopuma pseudopuma Günther

Hyla pseudopuma Günther, 1901 (1885-1902), p. 274 [syntypes, B.M.N.H. Nos. 96.10.8.61-67 from La Palma, San José Province, Costa Rica; C. F. Underwood collector; B.M.N.H. Nos. 1902.1.28.25-26 from La Palma, San José Province, Costa Rica; donated by the Museo Nacional de Costa Rica]. Taylor, 1952c, p. 871.

Hyla pseudopuma pseudopuma: Duellman, 1968a, p. 566.

DIAGNOSIS: This subspecies of *Hyla pseudopuma* is distinguished from *H. p. infucata* by having creamy tan or brown anterior and posterior surfaces of the thighs and webbing (red in *infucata*) and an acuminate snout (truncate in dorsal profile and bluntly rounded in lateral profile in *infucata*).

DESCRIPTION: Males of this subspecies attain a maximum known snout-vent length of 41.4 mm., and females reach 47.6 mm. In a series of 30 males from Tapantí, Cartago Province, Costa Rica, the snout-vent length is 37.6 to 41.4 (mean, 39.7) mm.; the ratio of tibia length to snout-vent length is 0.485 to 0.550 (mean, 0.515); the ratio of foot length to snout-vent length is 0.454 to 0.529 (mean, 0.482); the ratio of head length to snout-vent length is 0.296 to 0.333 (mean, 0.319); the ratio of head width to snout-vent length is 0.289 to 0.333 (mean, 0.312), and the ratio

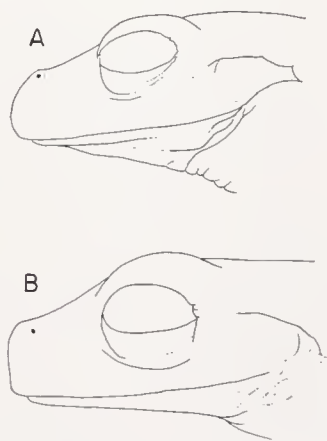


FIG. 115. Lateral views of the heads of (A) *Hyla p. pseudopuma* (K.U. No. 64884) and (B) *H. p. infucata* (K.U. No. 101784). $\times 3$.

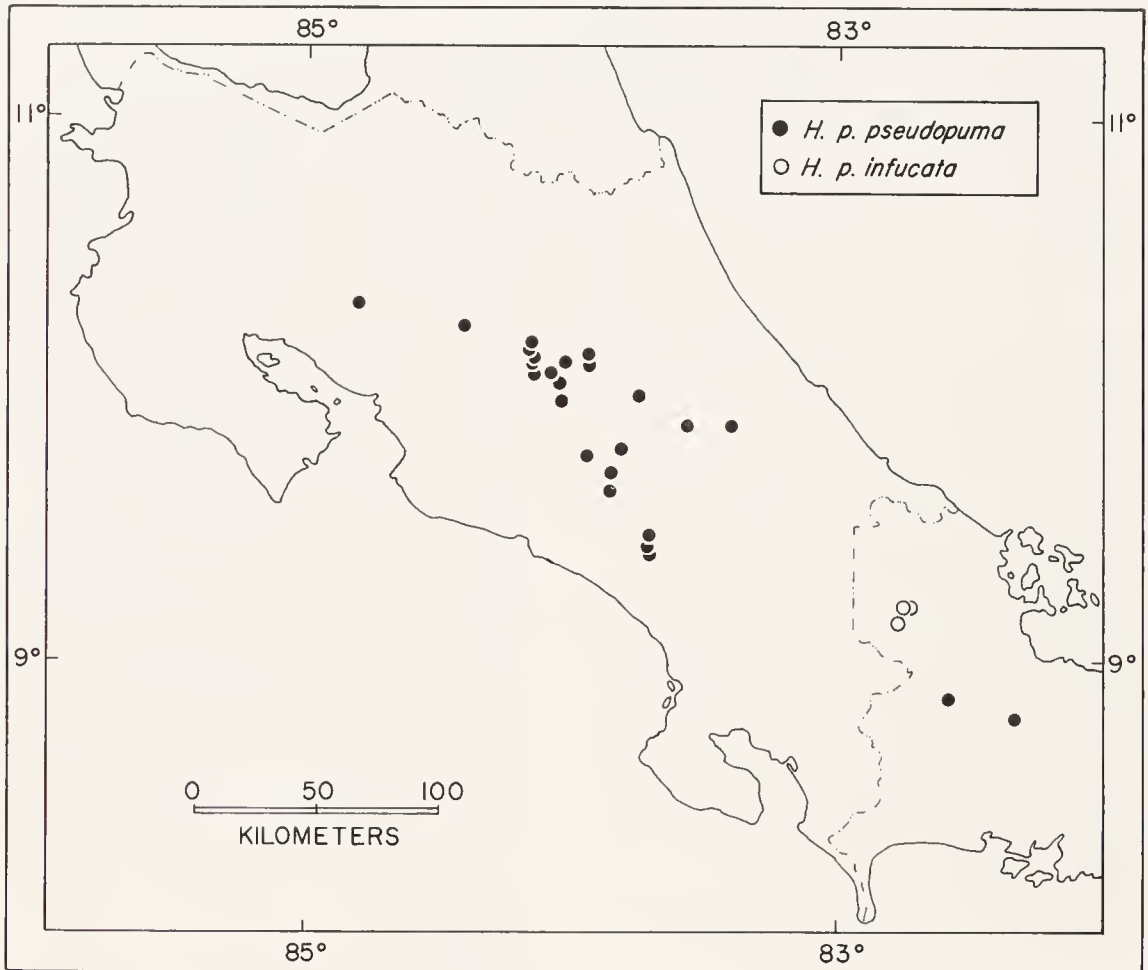


FIG. 116. Distribution of the subspecies of *Hyla pseudopuma*.

of the diameter of the tympanum to that of the eye is 0.476 to 0.667 (mean, 0.576). Eleven females from the same locality have snout-vent lengths of 41.6 to 47.6 (mean, 44.3) mm. and differ from the males only by having a slightly larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.579 to 0.714 (mean, 0.620).

The head is usually slightly narrower than the body, and the top of the head is barely convex. The snout in dorsal profile is acutely rounded; in lateral profile, it is rounded above and inclined to the margin of the lip in females, and gradually inclined in males (fig. 115A). The snout is moderately long; the slightly protruding nostrils are situated at a point about two-thirds of the distance from

the eyes to the tip of the snout; the internarial area is slightly depressed. The canthus is angular; the loreal region is barely concave, and the lips are moderately thick and slightly flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and robust; an axillary membrane is absent. A row of low tubercles is present on the ventrolateral edge of the forearm, and a thin dermal fold is present on the wrist. The hands are large, and the fingers are moderately long and robust

and bear large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and flattened; the distal tubercles on the third and fourth fingers are weakly bifid in many specimens. The supernumerary tubercles are large and numerous on the proximal segments of each digit. A small elevated palmar tubercle is present. The prepollex is greatly enlarged and bulbous and in breeding males bears an extensive horny nuptial excrescence. The fingers are about one-third webbed (fig. 117A). The webbing is vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third and from the distal end of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A thin transverse dermal fold is present on the heel, and a weak tarsal fold is present, at least distally. The inner metatarsal tubercle is small, elliptical, and flat. No distinct outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are moderately large and subconical, and the supernumerary tubercles are large, elevated, and pigmented. The toes are about two-thirds webbed (fig. 117C). The webbing extends from the middle of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroven- trally near the midlevel of the thighs. A short anal sheath is present, and a few large tubercles are present below the anal opening. The skin on the throat, belly, and proximal postero- ventral surfaces of the thighs is granular; else-

where, the skin is smooth. The tongue is cordi- form, shallowly notched posteriorly, and not free behind. The denticerous processes of the prevomers are narrowly separated, transverse or posteromedially inclined, high elevations between the posterior margins of the moder- ately small, quadrangular choanae. Males have four to six (mean, 4.8) and females have five to seven (mean, 5.8) teeth on each pro- cess. The vocal slits extend from the mid- lateral base of the tongue to the angles of the jaws. The vocal sac is median and subgular with a lateral expansion (fig. 118).

The general coloration of *Hyla pseudo- puma pseudopuma* is brown with darker brown markings on the dorsum and transverse bars on the limbs (pl. 52, fig. 5). The anterior and posterior surfaces of the thighs are tan or brown; the flanks are brown with yellow or creamy white spots. The venter is creamy white. The iris is deep bronze.

When active at night, most individuals are pale tan with brown or olive-brown markings on the dorsum and thighs and pale yellow spots on the flanks. By day, the dorsum in some individuals is pale gray or yellow with or without distinctive dark markings; the an- terior and posterior surfaces of the thighs are dark brown or black, and the flanks are dark brown or black with bright yellow spots. In some individuals, the axilla and groin are pale blue.

In preservative the dorsum is tan, reddish brown, or gray with darker markings. The variation in the dorsal pattern is considerable (fig. 119). In most males, there is a small amount of dark flecking on the edge of the chin and in some males there are brown spots on the skin. Most females have a heavy suf- fusion of brown or gray on the chin.

TADPOLES: Large developmental series of tadpoles are available from Tapantí, Cartago Province, and Río Las Vueltas, Heredia Prov- ince, Costa Rica. A typical tadpole in develop- mental stage 37 has a body length of 11.5 mm. and a total length of 31.0 mm. The body is robust, widest posteriorly, and only slightly wider than deep. In dorsal profile, the snout is round, and in lateral profile, it is inclined anteroventrally from the nostrils. The eyes are small, widely separated, and directed lat- erally. The nostrils are situated at a point

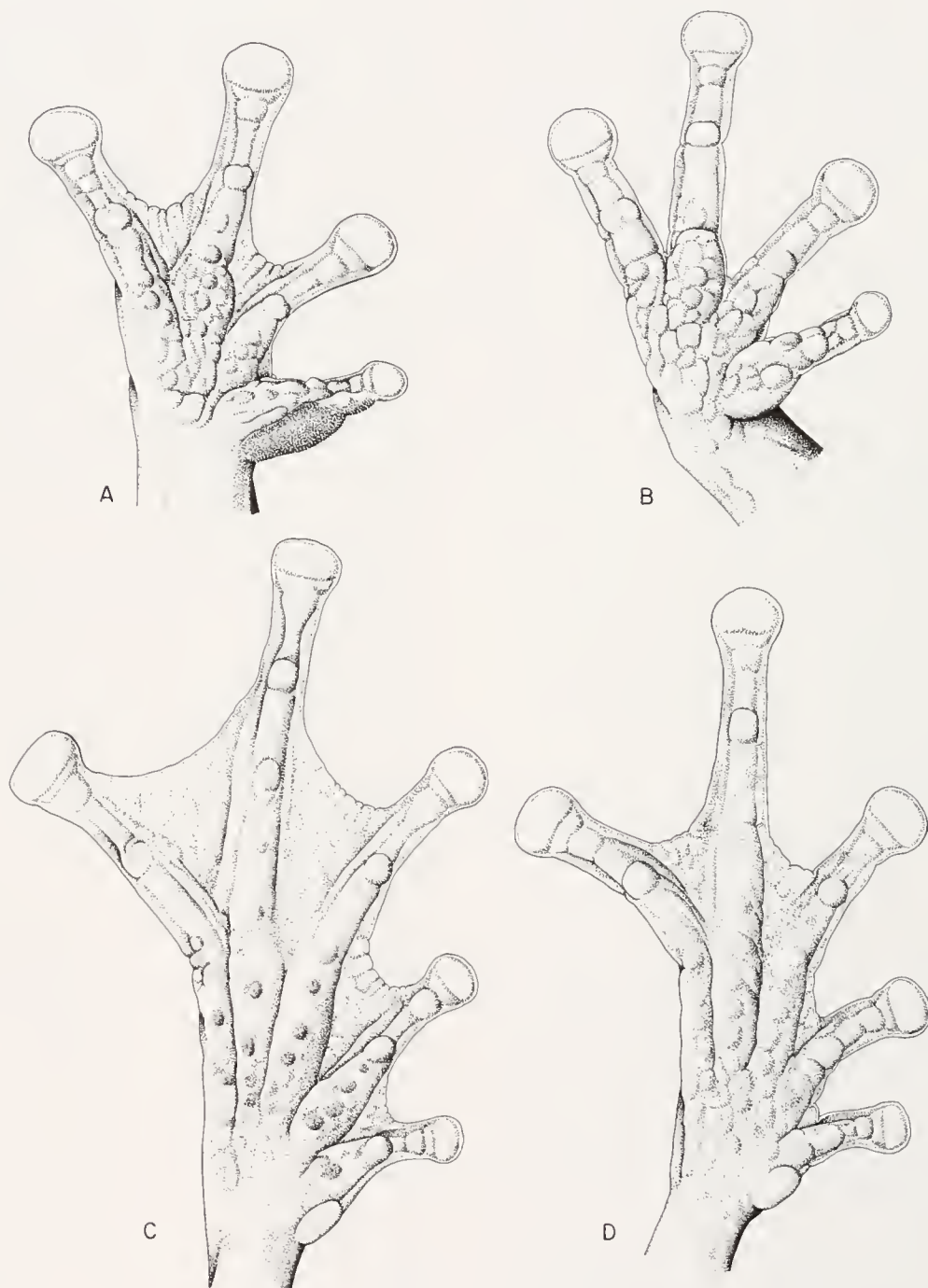


FIG. 117. Hands and feet of members of the *Hyla pseudopuma* group. A and C. *Hyla pseudopuma pseudopuma*, K.U. No. 103722. B and D. *Hyla angustilineata*, K.U. No. 103583. $\times 5$.



FIG. 118. Anterior view of the head of a male *Hyla p. pseudopuma* with vocal sacs expanded. $\times 3$.

about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point below the midline about two-thirds of the distance from the snout to the end of the body. The anal tube is short and dextral. The caudal musculature is relatively slender and terminates gradually just short of the tip of the rounded tail. The caudal fins are equal in depth, and the dorsal fin does not extend on to the body. At midlength of the tail, the depth of the caudal musculature is equal to the depth of either fin (fig. 120A).

The body is dark brown above and below, and the caudal musculature is brown. The fins are transparent but heavily flecked with brown. The iris is bronze. In preservative, the body is dark brown, and the caudal muscu-

lature is somewhat paler. The posteromedian part of the venter lacks pigment; elsewhere, the venter is heavily flecked with brown. There is a rather even distribution of brown flecks over the caudal fins.

The mouth is ventral and directed antero-ventrally. The mouth is relatively small and has weak lateral folds. The medial part of the upper lip is bare; otherwise, the mouth is bordered by two rows of small, conical papillae. Numerous papillae are present in the lateral folds. The beaks are well developed and bear small, pointed serrations. The upper beak is in the form of a broad arch with long, slender lateral processes. The ventral beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows extend laterally to the edge of the lip, and the first upper tooth row is narrowly interrupted medially. The lower rows are complete and nearly as long as the upper rows (fig. 121A).

The development of the tadpoles is discussed in the section on Natural History.

MATING CALL: The call of *Hyla p. pseudopuma* consists of a single, low, poorly modulated note or a series of short notes. Seemingly, the latter are nothing more than a fragmented longer note. In a recording of an individual producing normal notes, the note repetition rate is 45 notes per minute; the duration of each note is 0.03 of a second, and

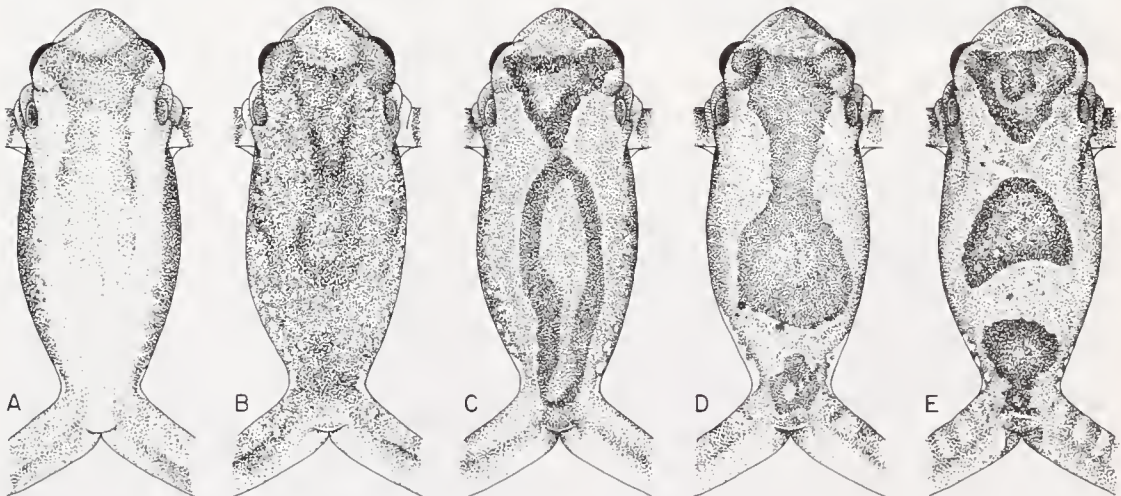


FIG. 119. Variation in dorsal color pattern in *Hyla pseudopuma pseudopuma*. A. K.U. No. 64866. B. K.U. No. 64893. C. K.U. No. 64889. D. K.U. No. 64902. E. K.U. No. 64879.

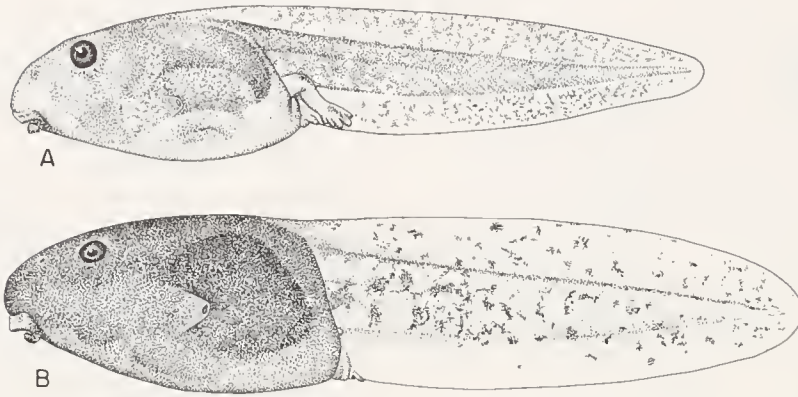


FIG. 120. Tadpoles of members of the *Hyla pseudopuma* group. A. *Hyla p. pseudopuma*, K.U. No. 104147. $\times 5$. B. *Hyla angustilineata*, K.U. No. 104120. $\times 3$.

the pulse rate is 85 pulses per second. The fundamental frequency is 69 cycles per second and the dominant frequency is 956 cycles per second (pl. 20, fig. 1).

NATURAL HISTORY: *Hyla pseudopuma*

pseudopuma inhabits humid montane areas in which the frog is active throughout the year. By day, the frogs are secreted in bromeliads or in elephant-ear plants. At night, when not breeding, individuals are found sitting on bushes and trees.

Apparently there are two breeding seasons each year in this species. Many mating pairs were found at Tapantí, Cartago Province, Costa Rica, on April 29, 1961. At the same locality from mid-May through July no mating activity was observed. Starrett (1960a, p. 22) noted that the species was breeding in large numbers on the southeast slope of Volcán Poás, Alajuela Province, Costa Rica, on August 6, 1957. I have observed calling males at Tapantí in late April and early May, at Cinchona, Alajuela Province, on April 5, and on the southeastern slopes of Cerro de la Muerte on April 7 and June 17. A biannual breeding season also is evidenced by the times of occurrence of recently metamorphosed young. Small young were found at Tapantí between June 6 and 29, 1961; many juveniles were found on March 30, 1966, at the Río Las Vuel-tas in Heredia Province, Costa Rica.

Prior to April 19, 1961, the only individuals of *Hyla pseudopuma* observed at Tapantí were taken from bromeliads and elephant-ear plants by day. On the night of April 19, after a light rain, many males were observed in muddy pools and depressions in a pasture at the edge of a forest; additional males and a few females were found on vegetation at the

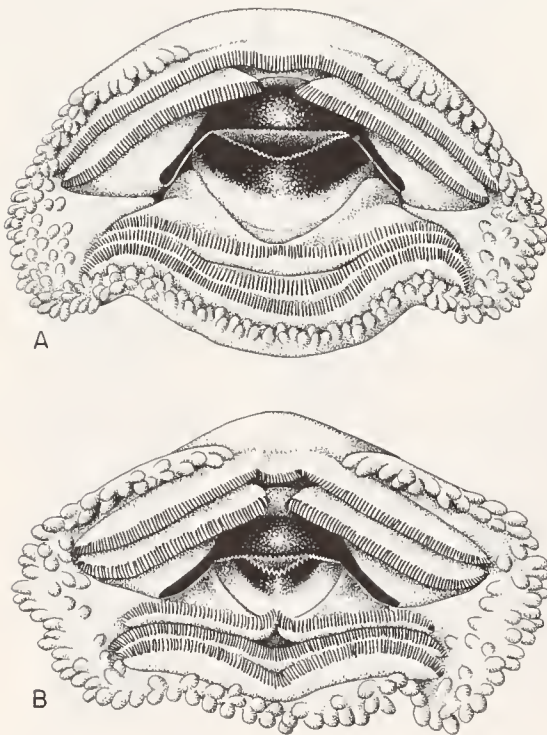


FIG. 121. Mouths of tadpoles of the *Hyla pseudopuma* group. A. *Hyla p. pseudopuma*, K.U. No. 104147. B. *Hyla angustilineata*, K.U. No. 104120. $\times 25$.

edge of the woods. No males were heard to call. On April 29, 1961, after a heavy rain in the afternoon, *Hyla pseudopuma* was extremely abundant at Tapantí. Many clasping pairs were found in muddy pools. Amplexus is axillary; the male rides far forward on the female, so that the snout of the male is nearly above the nostril of the female. The hind limbs of the male are tucked along the sides of the body. A few clasping pairs were observed on land. Of those pairs observed in the water, both males and females have the back arched. The female either has the hands free, usually in a downward position, or holding to a stick, leaf, or blade of grass. The eggs are exuded onto sticks, leaves, and blades of grass (pl. 8, fig. 1). During deposition, the female moves along a leaf, covers it with eggs, and moves to another object and keeps depositing eggs; thus, not all of the eggs are laid together. Many males were observed floating on the surface of the water with their hind limbs spread and the arms extended downward. In this position the back is slightly arched. The frogs are fast swimmers with the arms adpressed to the sides of the body. Similar observations

were made at the same locality on May 2, 1961.

Eggs collected on April 29, 1961, hatched the following day. Sixty hours after hatching, the tadpoles were in developmental stages 22 through 24. By 84 hours after hatching, all of the tadpoles were in developmental stage 25. During this stage the tadpoles grow, but do not begin the development of limb buds, which are first apparent in tadpoles 21 days of age. At an age of 35 days, most of the tadpoles were in developmental stages 30 and 31, and at an age of 70 days, the tadpoles varied from developmental stage 34 to stage 38. Some of the tadpoles metamorphosed on June 25, after only 57 days of development, whereas most of the tadpoles metamorphosed between July 17 and 19, thereby requiring 79 to 81 days to complete their larval development. The duration of the larval stage correlates well with observations made at Tapantí, where it is assumed that the first breeding possibly took place as early as April 19. Metamorphosing young were first observed on June 25 and again on June 29, thus indicating a period of 65 to 69 days for larval development.

TABLE 29

Measurements of Tadpoles, with Means in Parentheses, in Relation to Developmental Stages of *Hyla p. pseudopuma* from Tapantí, Costa Rica.

Stage	N	Body Length	Tail Length	Total Length
22	3	3.43- 3.50 (3.48)	4.13- 4.48 (4.27)	7.56- 7.98 (7.75)
24	3	3.46- 3.52 (3.50)	4.66- 4.72 (4.69)	8.12- 8.24 (8.19)
25	28	3.15- 5.25 (4.15)	4.20- 7.84 (5.65)	7.70-13.16 (9.84)
26	21	5.18- 7.00 (6.25)	7.56-10.00 (8.96)	12.74-17.00 (15.21)
27	15	6.58- 7.56 (7.08)	9.52-12.32 (10.64)	16.52-19.88 (17.72)
28	5	7.42- 8.40 (7.81)	11.06-12.32 (11.73)	18.48-20.72 (19.54)
29	3	8.12- 8.54 (8.31)	11.34-16.50 (13.34)	19.46-25.00 (21.63)
30	2	7.42- 8.10 (7.76)	14.00-15.90 (14.95)	21.42-24.00 (22.71)
31	5	7.42- 8.40 (7.93)	12.18-16.00 (14.84)	19.60-24.12 (22.76)
34	4	8.68- 9.80 (9.50)	17.50-17.90 (17.70)	26.58-27.50 (27.19)
35	2	9.60- 9.80 (9.70)	16.30-17.60 (16.95)	25.90-27.40 (26.65)
36	10	9.50-11.00 (10.15)	16.90-20.00 (18.20)	26.90-30.80 (28.36)
37	6	10.20-11.60 (10.63)	18.10-22.60 (19.92)	28.30-34.20 (30.55)
38	3	11.20-11.60 (11.43)	20.60-21.30 (20.97)	32.20-32.50 (32.40)
39	2	10.70-10.90 (10.80)	19.20-20.60 (19.90)	30.10-31.30 (30.70)
40	3	10.80-11.10 (10.97)	20.00-23.40 (21.33)	31.10-34.40 (32.30)
41	1	11.10	21.80	32.90
43	4	9.80-11.90 (11.03)	0.09- 7.00 (2.50)	9.80-18.90 (13.51)
46	27	10.36-13.72 (12.13)	-----	-----

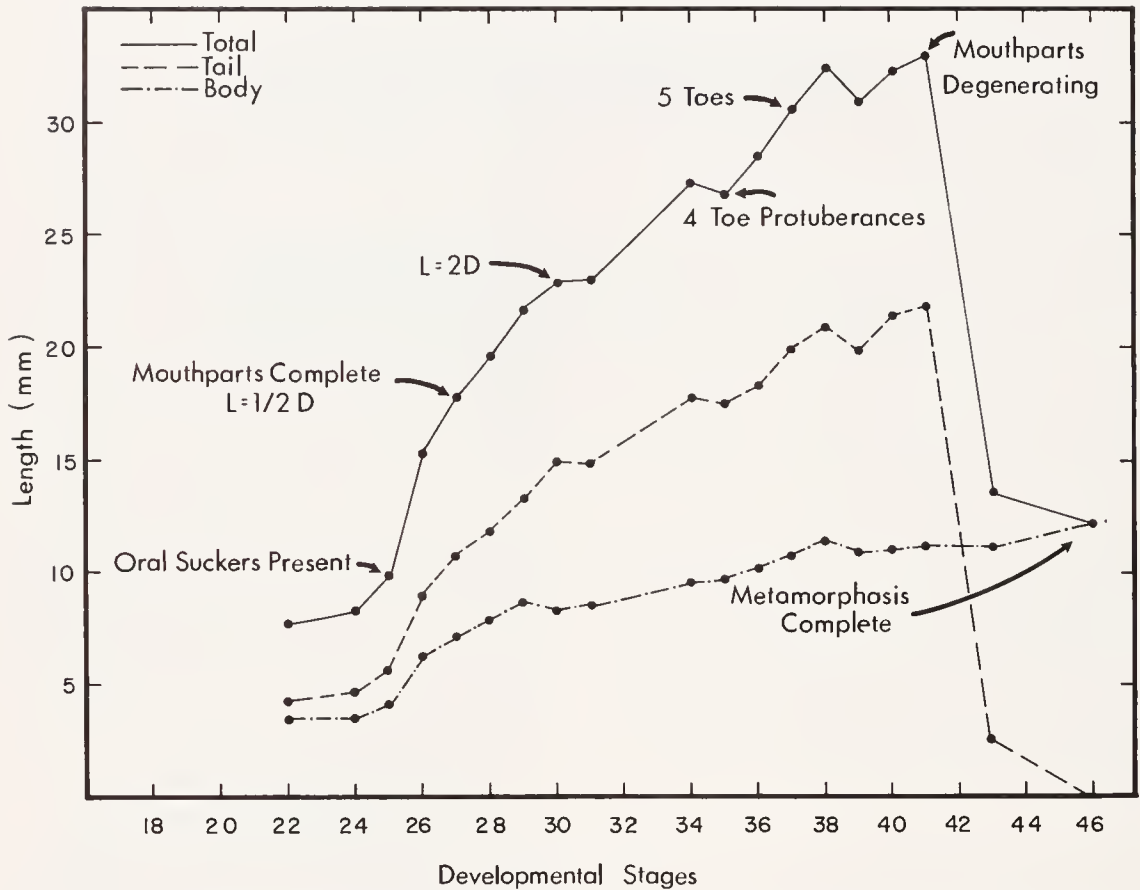


FIG. 122. Relative rate of growth in tadpoles of *Hyla pseudopuma* as correlated with developmental stages (table 29). Points are means of measurements given in table 2; formulas for the limb bud refer to its length (L) in relation to basal diameter (D).

The eggs are laid in an adherent mass, but the individual eggs and their membranes remain discreet. Ten eggs in developmental stages 5 through 8 have diameters of 1.62 to 1.85 (mean, 1.71) mm. The diameter of the fertilization membrane is 1.65 to 1.89 (mean, 1.75) mm., and the diameter of the outer envelope is 4.20 to 5.60 (mean, 4.95) mm.

The development and sizes of tadpoles are summarized in table 29 and figure 122. At hatching, the tadpoles are uniform brown in color. The tail bud is well developed, and the gill plate is furrowed. Three visceral arches are apparent. The oral suckers are well developed; the stomodeum is invaginated, but there is no evidence of invagination of the proctodeum. Tadpoles in developmental stage 20 have filamentous gills composed of about 13 unbranched divisions. The oral suckers are

still present but the cornea is not yet transparent. The tail is opaque, the myomeres are barely visible in the caudal musculature, and the dorsal fin seems to extend almost to the anterior end of the body. By developmental stage 22 the oral suckers are still well developed, although the mouth is beginning to form anteriorly. The caudal fins are not yet transparent; they seem to be covered with a fine pigment. In developmental stage 23, the gills are still present on both sides, and in most individuals, one oral sucker remains obvious and about ten times the size of the others. In the mouth, the beaks are formed, but there is no indication of tooth rows.

Small individuals in developmental stage 25 have remnants of oral suckers. The beaks are present and both upper tooth rows are faintly indicated; the second upper row is

widely interrupted medially. The first and second lower rows are present, and the first row is interrupted medially. The median part of the upper lip is bare, and the entire lower lip lacks papillae. In these tadpoles, the first indication of formation of color pattern is apparent. There is a moderate scattering of discreet arborized cells over the dorsal and lateral surfaces of the body and along the dorsal surface of the caudal musculature. The fins are finely pigmented. During developmental stage 25, the oral suckers completely disappear, and the mouthparts completely develop. The pigment becomes heavier over the dorsum, and the arborized cells aggregate to form blotches over the entire caudal musculature. The fins become transparent with brown flecks. Tadpoles in developmental stage 41 have lost the cloacal tail piece; the mouthparts are disintegrating. The third lower tooth row is absent, and the second row is only present in part. Tadpoles in developmental stage 45 have a well-developed adult mouth. The venter is unpigmented except for sparse flecking along the lateral edge of the lower jaw. The limbs are moderately pigmented in the form of transverse bands on the forearms and shanks.

In recently metamorphosed young, the dorsum is pale olive-tan with brown markings and pale tan spots. The lips are silvery white. The hind limbs are yellowish tan with brown bars, and the venter is silvery white.

REMARKS: *Hyla p. pseudopuma* is one of the most abundant frogs in the hylids of Costa Rica. Because of its apparent generalized morphology and life history, it would be useful to study more intensely the biology of this species.

ETYMOLOGY: The specific name is derived from the Greek *pseudes*, meaning false, and *puma*, an Indian name for a cat; the name *pseudopuma* is in reference to the species' general appearance to *Hyla (Smilisca) puma*.

DISTRIBUTION: *Hyla p. pseudopuma* occurs at elevations usually between 1000 and 2400 meters in the highlands of Costa Rica and on the Pacific slopes of western Panamá (fig. 116). On the Pacific slopes in Costa Rica, this species is known to descend to an elevation of 865 meters.

See Appendix 1 for the locality records of the 468 specimens examined.

Hyla pseudopuma infucata Duellman

Hyla pseudopuma infucata Duellman, 1968a, p. 564 [holotype, K.U. No. 101770 from the Río Changuena, Bocas del Toro Province, Panamá, 830 meters; William E. Duellman collector].

DIAGNOSIS: This subspecies of *Hyla pseudopuma* is distinguished from the nominate subspecies by having the webbing of the feet and the anterior and posterior surfaces of the thighs red, instead of tan or brown, and by having a truncate, instead of an acuminate snout.

DESCRIPTION: Males of this subspecies attain a maximum known snout-vent length of 42.9 mm., and females reach 45.6 mm. In a series of 30 males from the Río Changuena and Río Claro, Bocas del Toro Province, Panamá, the snout-vent length is 37.6 to 42.9 (mean, 39.5) mm.; the ratio of tibia length to snout-vent length is 0.504 to 0.569 (mean, 0.534); the ratio of foot length to snout-vent length is 0.433 to 0.495 (mean, 0.474); the ratio of head length to snout-vent length is 0.297 to 0.329 (mean, 0.319); the ratio of head width to snout-vent length is 0.289 to 0.335 (mean, 0.315), and the ratio of the diameter of the tympanum to that of the eye is 0.432 to 0.568 (mean, 0.492). Eleven females from the same area have snout-vent lengths of 41.1 to 45.6 (mean, 42.6) mm. In proportions, they differ from the males only by having a very slightly larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.435 to 0.561 (mean, 0.501).

Structurally, this subspecies is like the nominate subspecies, except for the shape of the snout and a slightly smaller tympanum (table 28). The snout in *Hyla pseudopuma infucata* is short and truncate; in lateral profile the snout is bluntly rounded, whereas in dorsal profile the snout is truncate. The canthus is rounded; the loreal region is barely concave and the lips are thick and moderately flared (fig. 115B).

The general coloration of *Hyla pseudopuma infucata* is brown above, creamy white below, and red on the hidden surfaces of the hind limbs and feet (pl. 52, fig. 6). In most individuals, the dorsum is yellowish tan with

olive-brown markings by night and uniform pale yellowish tan by day. The axilla, inner surface of the elbow, groin, anterior and posterior surfaces of the thighs, ventral surfaces of the thighs and shanks, inner surfaces of the feet, and dorsal surfaces of the first three toes are tomato red. The flanks are dark blue with yellow spots and reticulations. The throat, chest, and anterior part of the belly are creamy white, whereas the posterior part of the belly is orange, becoming red in the extreme posterior region. The throat is flecked with brown. The iris is pale bronze with black reticulations.

All specimens have the diagnostic red legs and blue flanks with yellow spots and mottling, but the dorsal pattern is highly variable. In most individuals the dark markings on the dorsum are a solid color, but in some specimens the borders of the marks are dark, and the interior of the mark is nearly the same color as the rest of the dorsum. A triangular dark mark with the anterolateral corners on the eyelids is present in all specimens. In some individuals, the posteriorly directed apex of this triangular mark is connected to the apex of another triangular mark on the back; in other individuals, the marks are narrowly separated, whereas in a few specimens, the marks are broadly connected. A dark blotch usually is present on the posterior end of the body. One specimen has many small white spots on the dorsum. A narrow transverse white stripe is present above the anus, and the transverse bars on the limbs are present in all specimens although they are indistinct in some individuals. The pattern on the flanks varies from three to four large spots to as many as 44 small spots. All males have dark flecks or reticulations on the throat; in some individuals, the chest and belly are heavily flecked. Although the amount of flecking is much less in most females, one individual is as heavily flecked on the throat and belly as any male.

There is considerable metachrosis in this frog. At night the frogs usually are yellowish tan above with slightly darker dorsal markings. The axilla, groin, and anterior and posterior surfaces of the thighs, ventral surfaces of the hind limbs, and webbing on the hands and feet are dark tomato red. By day, some individuals become creamy yellow, others

ashy white, and others grayish tan. The flanks are dark blue with yellow spots.

In preservative, the dorsum is grayish tan to brown with darker blotches on the back and transverse bands on the limbs. The anterior and posterior surfaces of the thighs are pinkish tan, and the webbing on the feet is pale gray. The flanks are brown with silvery white spots or reticulations. Numerous small white flecks are present on the heels and the proximal ventral surfaces of the thighs. The throat and belly are creamy white with brown flecks on the chin and in some individuals on the chest and belly.

TADPOLES: The tadpoles of this subspecies are unknown.

MATING CALL: No recordings of the call of this subspecies are available. Calls heard in the field are indistinguishable from those of the nominate subspecies.

NATURAL HISTORY: *Hyla pseudopuma infucata* inhabits humid lower montane forests characterized by high rainfall throughout the year. All of the known specimens were obtained from such forest. Most individuals were found on bushes and low trees at night, but three males and one clasping pair were found on the ground. Although no breeding was observed, it is presumed that this subspecies breeds in shallow, temporary pools, like those utilized by the nominate subspecies.

REMARKS: Although intergradation has not been demonstrated, the population here referred to as *Hyla pseudopuma infucata* certainly seems to be conspecific with *Hyla pseudopuma*. Both have the same kind of, and variation in, dorsal markings; furthermore, both taxa have conical, pigmented supernumerary tubercles on the toes, weakly bilobate vocal sacs, and greatly enlarged prepollices bearing horny nuptial excrescences.

ETYMOLOGY: The subspecific name is Latin, meaning painted and refers to the red colors on the limbs and web.

DISTRIBUTION: Presently *Hyla pseudopuma infucata* is known only from elevations between 830 and 910 meters on the Caribbean slopes of the Cordillera Talamanca in western Panamá (fig. 116).

See Appendix 1 for the locality records of the 50 specimens examined.

Hyla angustilineata Taylor

Hyla angustilineata Taylor, 1952c, p. 850 [holotype, U.S.N.M. No. 75060 from La Palma, San José Province, Costa Rica; M. Valerio collector].

DIAGNOSIS: This moderately small species has a brown dorsum (bright green in juveniles) with a sharply defined, bright, creamy yellow line from the tip of the snout, through the eye, to the groin, bordered below by a dark brown band. The venter is yellow flecked with black. Other Middle American *Hyla* having white dorsolateral stripes (*microcephala*, *picta*, *robertmertensi*, and *smithi*) are smaller and have a yellow or tan dorsum and lack dark flecks. *Hyla thorectes* and some populations of *Hyla lancasteri* have dark spots or mottling on the venter, but these species lack dorsolateral stripes.

DESCRIPTION: Males of this moderately small species attain a snout-vent length of 34.2 mm., and females reach 36.8 mm. In a series of 12 adult males from the Río Las Vueltas, on the south slope of Volcán Barba, Heredia Province, Costa Rica, the snout-vent length is 30.6 to 34.2 (mean, 31.5) mm.; the ratio of tibia length to snout-vent length is 0.492 to 0.554 (mean, 0.520); the ratio of foot length to snout-vent length is 0.411 to 0.451 (mean, 0.437); the ratio of head length to snout-vent length is 0.351 to 0.382 (mean, 0.362); the ratio of head width to snout-vent length is 0.352 to 0.375 (mean, 0.359), and the ratio of the diameter of the tympanum to that of the eye is 0.425 to 0.487 (mean, 0.456). Three females from the same locality have snout-vent lengths of 34.1 to 36.8 (mean, 35.1) mm. In proportions, they differ from the males only by having a slightly larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.450 to 0.536 (mean, 0.490).

The head is as wide as, or slightly wider than the body, and the top of the head is slightly convex. In dorsal profile, the snout is acutely rounded; in lateral profile it is round. The snout is moderately long; the nostrils are barely protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout; the internarial area is not noticeably depressed. The canthus is angular; the loreal region is barely concave, and the lips are moderately thick, but barely flared. A thin dermal fold extends posteriorly from the eye,

above the tympanum, to a point near the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance nearly equal to twice the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. There are a few small tubercles on the ventrolateral edge of the forearm, but these do not form a continuous row; a thin transverse dermal fold is present on the wrist. The hand is large; the fingers are moderately long and robust and bear large discs; the width of the disc on the third finger is slightly greater than the diameter of the tympanum. The subarticular tubercles are large and flattened; the distal tubercle on the fourth finger usually is bifid. The supernumerary tubercles are large and conical. A large elevated, bifid, palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrecence. The fingers essentially lack webbing (fig. 117B). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. Two small tubercles and a thin transverse dermal fold are present on the heel, but a distinct tarsal fold is lacking. An inner metatarsal tubercle is large, flat, and elliptical. The outer metatarsal tubercle is small and subconical. The feet are relatively small with short toes that have discs that are only slightly smaller than those on the fingers. The subarticular tubercles are relatively large and flattened, and the supernumerary tubercles are large, conical, and pigmented. The toes are about one-half webbed (fig. 117D). The webbing is vestigial between the first and second toes, but extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroven- trally just above the midlevel of the thighs. The anal sheath is short; several large tubercles are present below the anal opening. The

skin on the throat, belly and proximal postero-ventral surfaces of the thighs is strongly granular; elsewhere, the skin is smooth. The tongue is cordiform, shallowly notched posteriorly, and not free behind. The dentigerous processes of the prevomers are narrowly separated, transverse or posteromedially inclined, high elevations between the posterior margins of the moderately large ovoid choanae. Males have three to five (mean, 4.1) teeth on each process and a total of six to 10 (mean, 8.3) prevomerine teeth; females have four or five teeth on each process and a total of nine or 10 (mean, 9.3) prevomerine teeth. The vocal slits extend from the posterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla angustilineata* consists of a pale brown or olive-tan dorsum with a thin white dorsolateral line (pl. 52, fig. 3). The dorsum of the head and body is pale brown or olive-tan with a bronze hue. The lips are a bronze-tan. A thin white line extends from the tip of the snout, along the canthal ridge and edge of the upper eyelid and above the tympanum, to the insertion of the hind limb. The flanks are dark brown. The dorsal surfaces of the limbs are colored like the back and are marked by small dark brown spots. Numerous small brown spots usually are present on the back. The groin, ventral surfaces of the legs, anterior and posterior surfaces of the thighs, and the webbing on the feet are dull yellow. The throat and belly are creamy white. All ventral surfaces are heavily spotted with dark brown. The iris is reddish copper.

Juveniles having a snout-vent length of less than 25 mm. are colored noticeably different from the adults. The dorsum is bright leaf green and the dorsolateral stripe is white. The flanks are dark brown and the lips are pale green (pl. 52, fig. 4). The chin and belly are creamy white with black flecks. The limbs are tan with dark brown markings.

In preservative, the dorsum is dull brown or tan. The thin white stripe separates the dorsal color from the dark brown on the flanks. The dorsal surfaces of the limbs are pale brown with dark brown flecks or indications of

transverse marks. The venter is creamy tan, heavily flecked with brown.

TADPOLES: A typical tadpole in developmental stage 25 has a body length of 13.4 mm. and a total length of 33.1 mm. The body is robust, widest posteriorly, and as deep as wide. In dorsal profile, the snout is round; in lateral profile, it slopes gradually from the eye to a truncate tip. The eyes are small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point on the midline at about midlength of the body. The anal tube is short and dextral. The tail is short, slightly more than twice the length of the body. The caudal musculature is relatively slender and tapers gradually to a point just short of the rounded tip of the fin. The fins are moderately deep; the dorsal fin is slightly deeper than the ventral one and does not extend on to the body. At midlength of the tail, the depth of the caudal musculature is slightly less than the depth of either fin (fig. 120B).

The body is mottled brown and bronze-tan. The tail is creamy tan with dark brown markings on the musculature and fins. The iris is deep bronze. In preservative, the body is uniformly dark brown. The caudal musculature is cream with brown markings. The dorsal edge of the caudal musculature on the proximal half of the tail is dark brown. This gives the appearance of a narrow brown stripe when viewed laterally. Elsewhere, on the caudal musculature, the dorsal fin, and the posterior one-third of the ventral fin, there are small brown flecks.

The mouth is relatively small and directed ventrally. Shallow lateral folds are present in the lips, which are bare anteromedially, but elsewhere bordered by two rows of small papillae. The beaks are well-developed and bear short, pointed serrations. The upper beak is in the form of a broad arch with long, slender lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are long, and the second upper row is narrowly interrupted medially. The three lower rows are

equal in length, but shorter than the upper rows, and complete (fig. 121B).

MATING CALL: The call of *Hyla angustilineata* consists of a pair of short, pulsed, poorly modulated notes. In the one recording available, the interval between call groups varies from 72 to 80 seconds. The duration of each note varies from 0.07 to 0.14 of a second. The notes have 90 pulses per second, a fundamental frequency of 87 cycles per second, and a dominant frequency of 1653 cycles per second (pl. 20, fig. 2).

NATURAL HISTORY: *Hyla angustilineata* inhabits humid upper montane forests, where it breeds in water-filled depressions. In March and April, 1966, males were calling sporadically around water-filled depressions in an overgrown meadow adjacent to oak forest on

Volcán Barba. The presence of numerous tadpoles in the ponds at that time, as well as the presence of several recently metamorphosed young, indicates that this species either breeds more than once each year or that the breeding season had long since past in this species. However, in April, 1966, one gravid female was obtained.

Seven recently metamorphosed young have snout-vent lengths of 15.1 to 18.9 (mean, 17.4) mm.; they were colored like the juveniles described previously.

REMARKS: The tadpoles of this species are extremely generalized, like those of *Hyla pseudopuma*. On the basis of larval structure and the generalized cranial features, *Hyla angustilineata* has been grouped with *Hyla pseudopuma*.

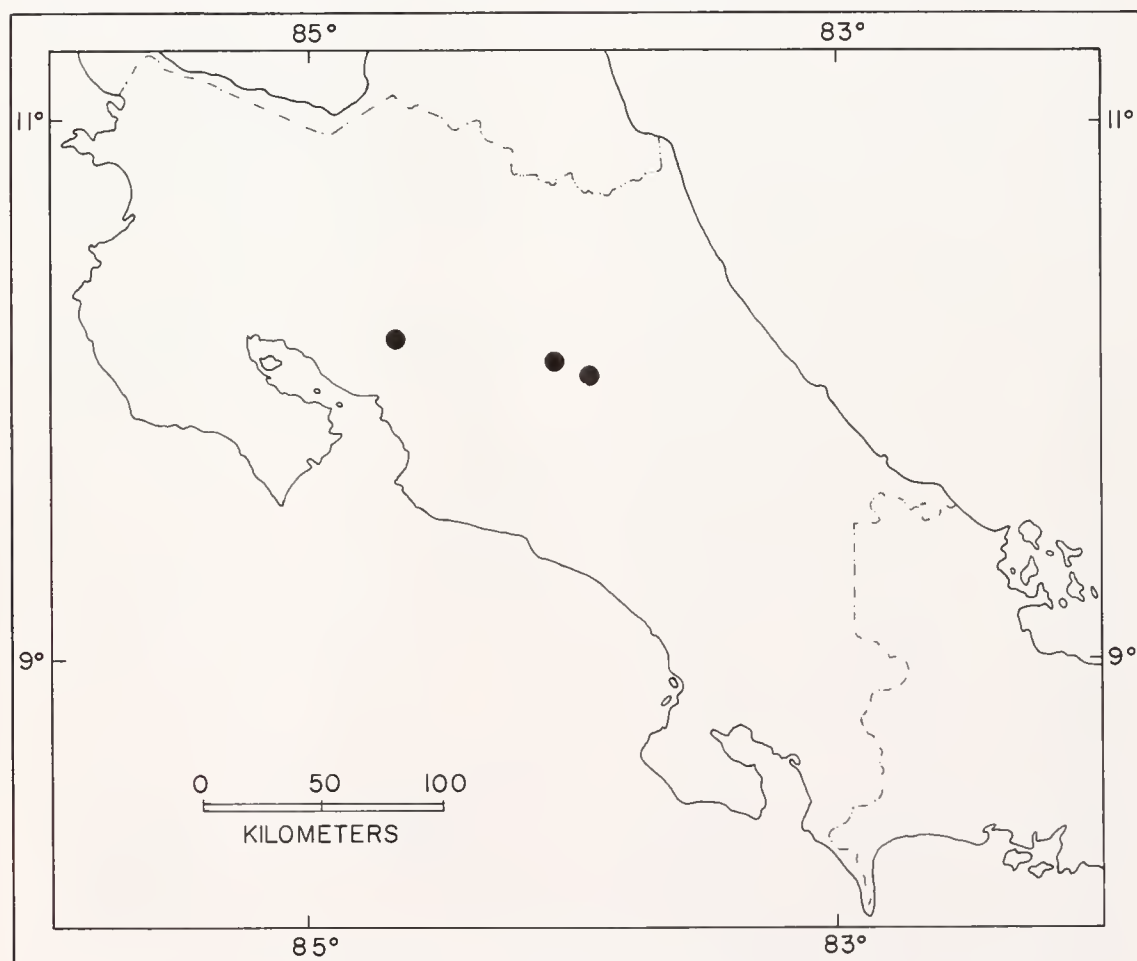


FIG. 123. Distribution of *Hyla angustilineata*.

ETYMOLOGY: The specific name is derived from the Latin *angustus*, meaning narrow, and the Latin *lineatus*, meaning of a line, and refers to the narrow dorsolateral line characteristic of this species.

DISTRIBUTION: *Hyla angustilineata* is known from three localities (elevations between 1500 and 2200 meters) in humid montane forests in the Cordillera Central of Costa Rica (fig. 123).

See Appendix 1 for the locality records of the 36 specimens examined.

The *Hyla rivularis* Group

DEFINITION: The members of this group are small, stream-breeding species; males attain a maximum snout-vent length of 34 mm. and females, 43 mm. The dorsum is green, tan or mottled dark green and black. The posterior surfaces of the thighs are yellow or dark brown with or without contrasting markings. The palpebral membrane is clear. The fingers are no more than one-third webbed, and the toes are about two-thirds webbed. Dermal fringes and appendages are lacking on the limbs, and a distinct axillary membrane is absent. Males have single, median, subgular vocal sacs and horny nuptial excrescences on the pollices. The cranial elements are moderately well-ossified; a large frontoparietal fontanelle is present, and the sphenethmoid is large and extends anteriorly between the nasals. The quadratojugal is absent or reduced to a small spur. The nasal lacks a maxillary process, and the pterygoid does not have a bony articulation with the prootic. Prevomerine teeth are present. The tadpoles have a long, terminally rounded tail and a large, ventral mouth with deep lateral folds and two upper and three lower rows of teeth. The mating call consists of series of short, quickly repeated notes. The haploid number of chromosomes is 12 (known only in *H. rivularis* and *tica*).

COMPOSITION: Four species (*H. debilis*, *rivularis*, *tica*, and *xanthosticta*) comprise the group, which is endemic to lower Central America. All of the species, as now recognized, are monotypic. Of the four species, 421 preserved frogs, nine skeletons, and 27 lots of tadpoles were examined.

COMMENTS: Starrett (1966) suggested

that *Hyla debilis*, *pictipes*, *rivularis*, and *tica* comprised one species group, that possibly also included *Hyla legleri*, *rufiocularis*, and *uranochroa*. Duellman (1968a) named *H. xanthosticta* and placed the new species in the *Hyla pictipes* group. Consideration of osteological and larval features, plus characteristics of the mating calls has necessitated the recognition of three groups of species, all of which were tentatively placed in the *Hyla pictipes* group by Starrett.

Hyla pictipes differs from the four species here included in the *Hyla rivularis* group by having a broader skull with a smaller frontoparietal fontanelle (a consequence of medial growth of the frontoparietals), a much shorter sphenethmoid that does not extend anteriorly between the nasals, and a more slender pterygoid (figs. 124 and 133). Furthermore, the mating call of *pictipes* is a single, pulsed, low-pitched note, noticeably different from the series of short, rather high-pitched notes produced by members of the *Hyla rivularis* group.

The *Hyla uranochroa* group has different larval and osteological conditions; the iris is red, and the mating calls are different from

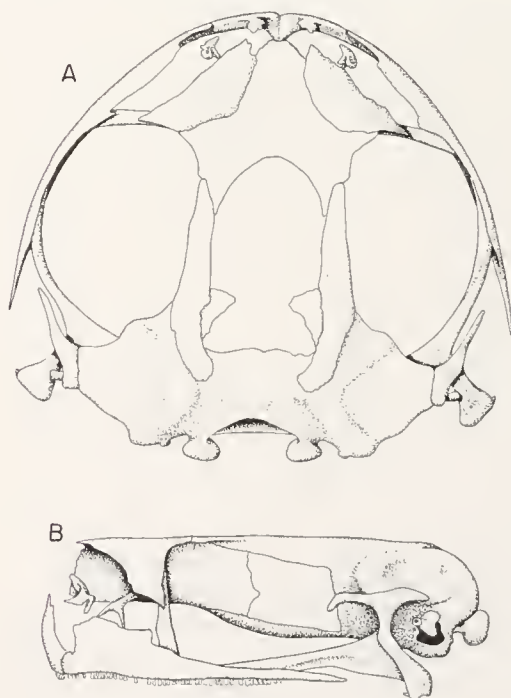


FIG. 124. Dorsal (A) and lateral (B) views of the skull of *Hyla tica*, K.U. No. 77691. $\times 7$.

the *Hyla rivularis* group and *Hyla pictipes* (see definition of the *Hyla uranochroa* group for details).

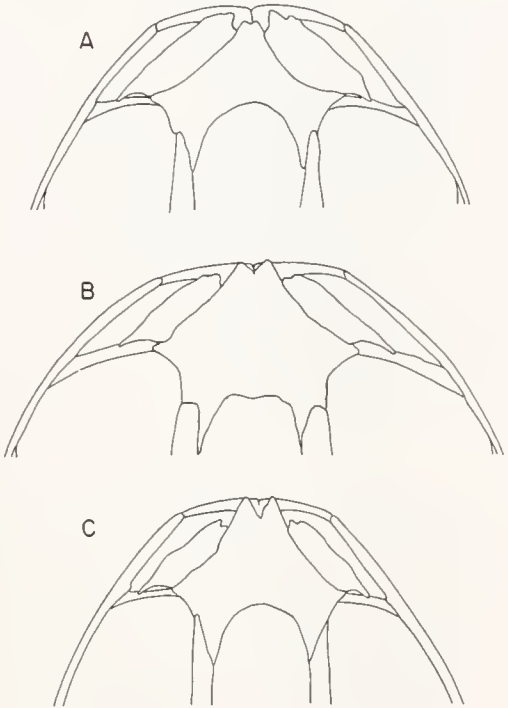


FIG. 125. Dorsal views of the anterior part of the skulls of members of the *Hyla rivularis* group showing the position and shape of the sphenethmoid. A. *H. tica*, K.U. No. 77691. B. *H. rivularis*, K.U. No. 68610. C. *H. debilis*, K.U. No. 104323. Approx. \times 5.

Thus, I conclude that although *Hyla pictipes* is related to the *Hyla rivularis* group, *pictipes* represents a divergent line from the *Hyla rivularis* group-stock. *Hyla tica* seems to be the most primitive member of the group. This supposition is supported by its relatively short sphenethmoid, more variable mating call, and broad altitudinal distribution. The other species in the group can be derived from *Hyla tica* by a decrease in size (table 30), increase in length of the sphenethmoid (fig. 125), and divergence of the mating call into the lower (*rivularis*) and higher (*debilis*) frequencies (table 31, pl. 2). The anterior extension of the sphenethmoid in *rivularis* and *debilis* is reflected externally in the angularity of the protruding snout in these species, whereas the snout is round in *tica*. The structure of the hands and feet is nearly alike in the four species, most of which have a double or bifid distal subarticular tubercle on the fourth finger (figs. 126 and 127). Few structural differences exist among the tadpoles (figs. 128 and 129). The geographical distribution of *Hyla tica* encompasses the known ranges of the other species, except for the apparent absence of *tica* on the Atlantic slopes in western Panamá, an area included in the ranges of *debilis* and *rivularis*.

The four species are partially segregated altitudinally. *Hyla debilis* occurs at moderate

TABLE 30
Comparison of Sizes and Certain Proportions, with Means in Parentheses, of the Species
in the *Hyla rivularis* Group.

Species	Sex	N	Snout-vent Length	Tibia Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
<i>H. tica</i>	♂	38	27.4-34.1 (31.8)	0.493-0.527 (0.511)	0.297-0.336 (0.323)	0.462-0.594 (0.517)
	♀	12	33.6-42.7 (37.6)	0.497-0.521 (0.508)	0.289-0.340 (0.324)	0.514-0.588 (0.542)
<i>H. rivularis</i>	♂	25	29.9-34.0 (32.3)	0.443-0.489 (0.463)	0.311-0.334 (0.323)	0.303-0.455 (0.367)
	♀	6	33.4-36.4 (35.7)	0.439-0.482 (0.460)	0.316-0.329 (0.328)	0.361-0.455 (0.409)
<i>H. debilis</i>	♂	20	25.1-29.5 (26.6)	0.461-0.515 (0.485)	0.284-0.328 (0.308)	0.452-0.593 (0.535)
	♀	5	26.8-31.6 (29.9)	0.452-0.499 (0.476)	0.287-0.331 (0.316)	0.485-0.581 (0.538)
<i>H. xanthosticta</i>	♀	1	29.3	0.553	0.352	0.500

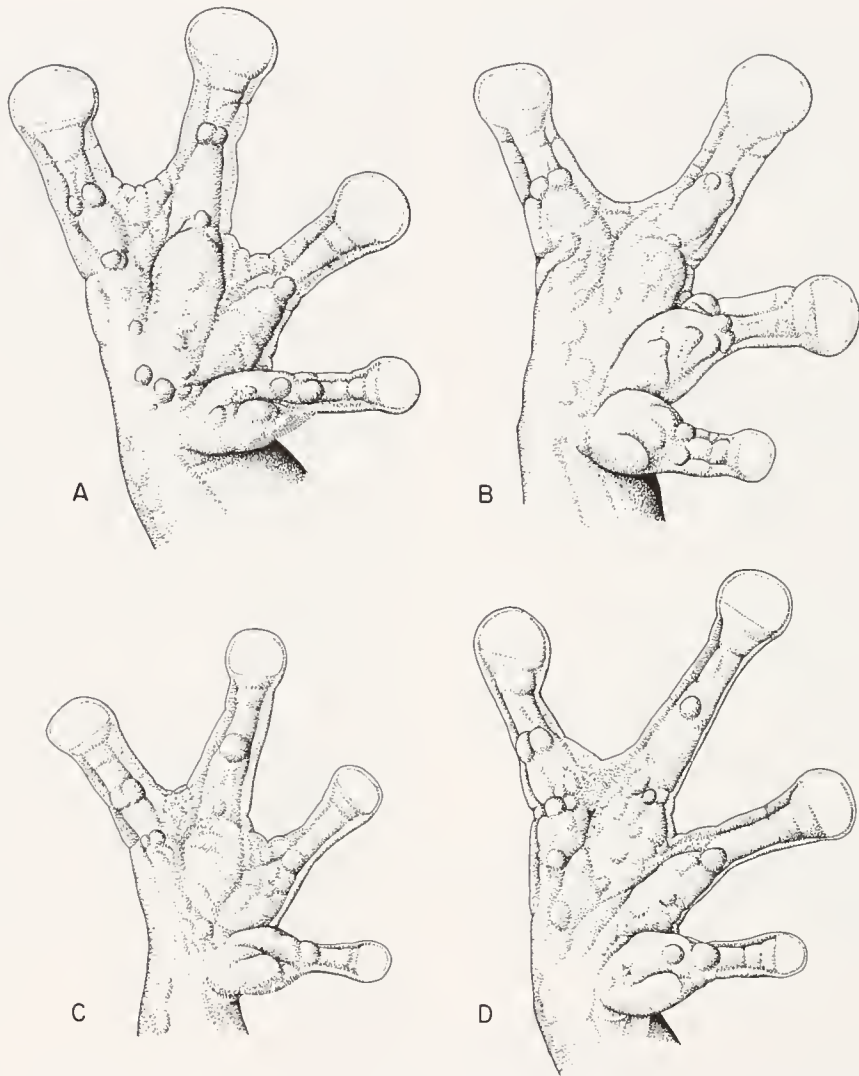


FIG. 126. Hands of the species of the *Hyla rivularis* group. A. *H. tica*, K.U. No. 103760. B. *H. rivularis*, K.U. No. 103735. C. *H. debilis*, K.U. No. 101567. D. *H. xanthosticta*, K.U. No. 103772. $\times 6$.

elevations (910 to 1450 meters), whereas *rivularis* occurs at elevations of 1280 to 2840 meters and *tica* at 835 to 1920 meters; *Hyla xanthosticta* is known only from one locality at 2100 meters on Volcán Barba, Costa Rica. Although their altitudinal distributions narrowly overlap, I do not know of *rivularis* and *debilis* having been found sympatrically. *Hyla tica* occurs sympatrically with *rivularis* and *debilis*, and *rivularis* occurs at the only locality where *xanthosticta* has been found.

Hyla tica Starrett

Hyla tica Starrett, 1966, p. 23 [holotype, U.M.M.Z. No. 122482 from a stream on Volcán Turrialba, Cartago Province, Costa Rica, 1400 meters; Andrew and Priscilla Starrett and Thomas M. Uzzell, Jr. collectors].

DIAGNOSIS: *Hyla tica* differs from other members of the *Hyla rivularis* group by having a tuberculate dorsum, mottled dorsal coloration, distinct transverse bands on the limbs, and rounded snout in lateral profile. *Hyla pictipes* is similar in general appearance but has



FIG. 127. Feet of the species of the *Hyla rivularis* group. A. *H. tica*, K.U. No. 103760. B. *H. rivularis*, K.U. No. 103735. C. *H. debilis*, K.U. No. 101567. D. *H. xanthosticta*, K.U. No. 103772. $\times 6$.



FIG. 128. Tadpoles of the species of the *Hyla rivularis* group. A. *H. tica*, K.U. No. 104127. B. *H. rivularis*, K.U. No. 104156. C. *H. debilis*, K.U. No. 104239. $\times 3$.

an acutely angular snout in lateral profile and dark flanks and posterior surfaces of the thighs with creamy white or yellow spots, instead of dull tan posterior surfaces of the thighs and mottled flanks. Furthermore, the tympanum is much smaller in *pictipes* than in *tica*; the average ratio of the diameter of the tympanum to that of the eye in *pictipes* is 0.377 and in *tica*, 0.517. Other Middle American hylids that might be confused with *tica* are *Hyla lancasteri*, *Smilisca baudinii* and *S. sila*. Each of these has a barred lip and more webbing in the hand. The former has bold black spots on the flanks and thighs; *Smilisca* has paired subgular vocal sacs, and *S. baudinii* has creamy yellow flanks with black mottling, whereas *S. sila* has small blue spots on the flanks and posterior surfaces of the thighs.

DESCRIPTION: This is the largest species in the *Hyla rivularis* group. Males attain a maximum snout-vent length of 34.1 mm. (mean, 21 specimens from central Costa Rica, 31.6 mm.), and females reach a maximum snout-vent length of 42.7 mm. (mean, six specimens from central Costa Rica, 38.9 mm.). In the

sample of males from central Costa Rica, the ratio of tibia length to snout-vent length is 0.493 to 0.527 (mean, 0.511); the ratio of foot length to snout-vent length is 0.435 to 0.477 (mean, 0.453); the ratio of head length to snout-vent length is 0.294 to 0.327 (mean, 0.308); the ratio of head width to snout-vent length is 0.297 to 0.336 (mean, 0.323), and the ratio of the diameter of the tympanum to that of the eye is 0.462 to 0.594 (mean, 0.517). There is no apparent geographic variation in size and proportions; specimens from western Panamá are essentially like those from central Costa Rica. Females are noticeably larger than the males; the smallest female (snout-vent length, 33.6 mm.) is only slightly smaller than the largest male (snout-vent length, 34.1 mm.).

The head is slightly narrower than the body and slightly longer than wide; the top of the head is barely convex. The snout is short, acutely rounded in dorsal profile and bluntly rounded in lateral profile. The nostrils are barely protuberant and are situated about three-fourths the distance from the eyes to

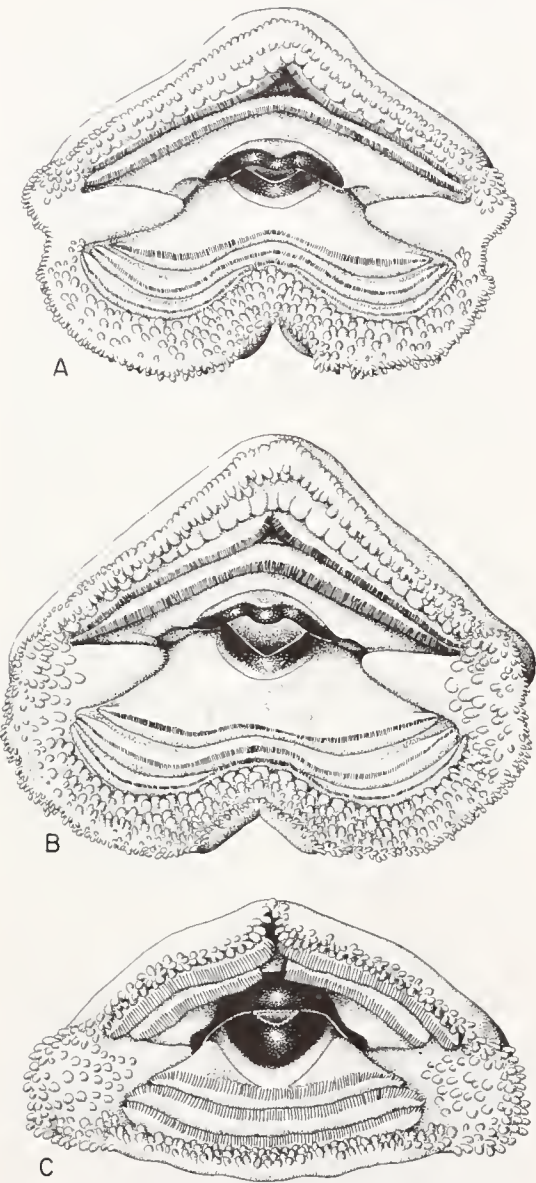


FIG. 129. Mouths of tadpoles of the species of the *Hyla rivularis* group. A. *H. tica*, K.U. No. 104127. B. *H. rivularis*, K.U. No. 104156. C. *H. debilis*, K.U. No. 104239. $\times 12$.

the tip of the snout. The canthus is angular and distinct; the loreal region is deeply concave, and the lips are moderately thick and flared. A heavy supratympanic fold extends from the posterior corner of the eye to a point above the insertion of the arm; a thinner der-

TABLE 31
Characteristics of Mating Calls, with Means in Parentheses, of Frogs in the *Hyla rivularis* Group.

Species	N	Notes per Call Group	Duration Call Group (seconds)	Repetition Rate Call Group (seconds)	Pulses per Call	Dominant Frequency (cps)	Emphasized Harmonic (cps)
<i>H. tica</i>	5	3-5 (3.8)	0.38-0.60 (0.50)	1.0-4.5 (1.6)	2-4 (3.1)	1980-2300 (2228)	4420-4840 (4752)
<i>H. rivularis</i>	7	12-137 (34.3)	5.0-66.0 (16.2)	10.0-70.0 (21.2)	3	2160-2880 (2420)
<i>H. debilis</i>	8	5-7 (5.9)	0.10-0.16 (0.12)	0.45-0.60 (0.50)	1	4800-5360 (5235)

mal fold extends from the angle of the jaw to the posterior terminus of the supratympanic fold. The upper edge of the tympanum is covered by the supratympanic fold; otherwise, the tympanum is distinct. The tympanum is situated posterior to the eye and is separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately long and robust. A moderate axillary membrane is present, but a thoracic fold is lacking. A tuberculate dermal ridge is present on the ventrolateral edge of the forearm and the fourth finger; a distinct transverse fold is present on the wrist. The fingers are short and broad and bear large discs; the width of the disc on the third finger is half again the size of the diameter of the tympanum. The subarticular tubercles are moderately small and conical. The distal tubercle on the fourth finger is divided in all specimens, whereas that on the third finger is either divided or bifid. A few moderately large, subconical supernumerary tubercles are present on the proximal segments of the third and fourth fingers. Two small, distinct outer palmar tubercles are present. The prepollex is moderately enlarged and in breeding males bears a small, brown, horny nuptial excrescence. The fingers are about one-third webbed (fig. 126A). Only a vestige of a web is present between the first and second fingers; the web extends from the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels barely overlap. The tibiotarsal articulation extends to the anterior corner of the eye. A tarsal fold is lacking. In some specimens a few small tubercles form a row along the outer edge of the tarsus. The inner metatarsal tubercle is low, barely rounded, and ovoid; it is broadly visible from above. A small, conical outer metatarsal tubercle is present. The toes are moderately long and robust and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are large and round; small, subconical supernumerary tubercles are present on the proximal segments of all digits. The toes are about two-thirds

webbed (fig. 127A). The web extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, and from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth, and from the base of the penultimate phalanx of the fourth to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the mid-level of the thighs and is covered by a short anal sheath. The skin on the dorsal surfaces is smooth with many low, rounded tubercles, that are especially numerous in the occipital and sacral regions. The skin on the throat, belly, and posteroventral surfaces of the thighs is granular, whereas that on the other ventral surfaces is smooth. The tongue is cordiform, nearly as broad as long, shallowly notched posteriorly, and barely free behind. Males have a total of seven to 11 (mean, 9.0) prevomerine teeth, and females have 13 or 14 (mean, 13.3) prevomerine teeth situated on small transverse ridges between the posterior margins of the small, triangular choanae. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and not greatly distensible.

The general coloration of *Hyla tica* is mottled green and brown dorsally with distinct brown transverse bands on the limbs (pl. 53, fig. 1). The dorsal ground color varies from a pale olive-green to tan. The dorsal markings consist of small, irregularly-shaped blotches, many of which usually are interconnecting, and small dark brown flecks. The flanks are dark brown with grayish white spots or tan or greenish tan with dull white spots that are narrowly surrounded by dark brown. There are four or five narrow dark transverse bands on the thigh, three or four bands on the shank and two or three on the tarsus and forearm. The posterior surfaces of the thighs are brown, orange-brown, or tan, with or without yellowish tan flecks on the posterodorsal surface. The lips are dull olive-brown or dark brown with grayish white or greenish white spots along the margin. The venter is dull white,

usually with a gray suffusion, especially on the chest and laterally on the belly. The iris is dull reddish bronze.

When active at night, the dorsum is either dull tan or dark brown with scattered metallic green flecks. By day the green pigment expands to form the coloration described above. Specimens from the eastern part of the range, in western Panamá, usually have the posterior surfaces of the thighs a darker color, that is brown or orange-brown, than do those specimens from central Costa Rica, where the posterior surfaces of the thighs are tan or yellowish tan. However, some individuals from central Costa Rica have dark brown posterior surfaces of the thighs; in some of these, yellowish tan flecks are present.

In preservative, the dorsum is pale brown or grayish brown with darker brown markings. The white spots persist on the flanks. The venter is dull creamy white with a grayish suffusion.

TADPOLES: The largest tadpole available is in developmental stage 43 and has a body length of 15.0 mm. and a total length of 40.5 mm. A typical tadpole in developmental stage 34 from Tapantí, Cartago Province, Costa Rica, has a total length of 37.7 mm. and a body length of 12.0 mm. The body is depressed and much wider than deep; it is widest just behind the eyes. In dorsal profile the snout is broadly rounded, and in lateral profile it is acuminate. The nostrils are directed anterodorsally and are situated about midway between the eyes and the tip of the snout. The eyes are small and directed dorsolaterally. The mouth is large and directed ventrally. The belly is flat. The spiracle is sinistral and situated ventrolaterally about midway between the eye and the posterior edge of the body. The anal tube is short and dextral. The tail is long, three times the length of the body, shallow, but with heavy caudal musculature, which in dorsal view does not grade gradually into the body, but is distinctly demarked from the posterior edge of the body. The fins are shallow, and at midlength of the tail the caudal musculature is deeper than either of the caudal fins. The dorsal fin does not extend onto the body, and posteriorly the caudal fins are rounded. The caudal musculature is robust throughout its length and terminates just

before the end of the caudal fin (fig. 128A).

The body is brown above and silvery gray below. The snout is tan. The tail is creamy tan with brown transverse markings dorsally and brown reticulations laterally. The fins are transparent with brown flecks, except on the anterior half of the ventral fin. The iris is bronze. In preservative, the body is dull brown above and transparent below. The tail is creamy white with grayish brown markings.

The mouth is large and as wide as the body. Well-developed lateral folds are present. The mouth is completely surrounded by labial papillae; two small rows and one internal large row are present on the upper lip, and four to six rows of papillae are present on the lower lip; only one row of papillae is present laterally, and the lateral folds are devoid of papillae. The beaks are slender; the upper beak is in the form of a broad arch that is indented medially and lacks lateral processes; the lower beak is broadly V-shaped. Both beaks bear minute serrations. There are two upper and three lower rows of teeth. The teeth in the upper rows are larger than those in the lower rows; all of the rows are approximately equal in length and are complete (fig. 129A).

MATING CALL: The call of *Hyla tica* consists of a series of cricket-like chirps. Each call group consists of three to five notes and the call groups are repeated at intervals of about 1.5 seconds. There are two to four pulses in each call. In the audiospectrograms, several harmonics are visible; two of these (approximately at 2225 and 4750 cycles per second) are emphasized nearly equally (pl. 21, fig. 1).

NATURAL HISTORY: *Hyla tica* inhabits cloud forests. In these moist environments, the frogs apparently are active throughout the year. Individual frogs have been found on vegetation at the edges of streams in both the rainy season and the dry season, but breeding activity seems to be concentrated in the drier months of the year. Calling males and gravid females have been obtained in February, March, and April. The males call from rocks in the streams or from the branches of bushes and trees overhanging the streams. Usually calling males are found only above fast

stretches of water; they usually are absent from the borders of quiet pools in the streams.

Tadpoles were found in a small, rocky, gravel-bottomed stream at Tapantí, Cartago Province, Costa Rica, on March 26, 1966. The tadpoles adhered to the lee sides of rocks on the bottom of pools. When the tadpoles were disturbed, they moved away rapidly to another rock or took shelter in the debris at the bottom of the pool. Metamorphosing young have been found at Tapantí on April 19, April 29, and June 6. These juveniles were found on leaves of bushes near the stream at night. One completely metamorphosed individual had a snout-vent length of 18.4 mm.; five individuals having tail stubs five to 11 mm. in length had snout-vent lengths of 17.3 to 19.3 (mean, 18.3) mm. The completely metamorphosed individual had a dark brown dorsum with metallic green flecks. The dorsal surfaces of the limbs were coppery tan with dark brown bands. The flanks, anterior and posterior surfaces of the thighs, and ventral surfaces of the limbs were yellow. The belly was yellowish white, and the chest, throat, and upper lips were white.

As noted by Starrett (1966) the females contained large (2 mm.) unpigmented eggs. Probably the eggs are deposited in the streams.

REMARKS: *Hyla tica* seemingly replaces *Hyla pictipes* at lower elevations. The two species have not been collected along the same stream. Contrariwise, *Hyla tica* altitudinally overlaps the distribution of *Hyla rivularis* and *debilis*. At Cinchona, Alajuela Province, Costa Rica and at several localities in Chiriquí Province, Panamá, *Hyla tica* and *rivularis* have been found breeding at the same time in the same stream. Likewise, *Hyla tica* and *debilis* breed in the same stream at Tapantí, Costa Rica.

ETYMOLOGY: The specific name *tica* is derived from the local name "tico," used for the inhabitants of Costa Rica.

DISTRIBUTION: *Hyla tica* inhabits the cloud forests and lower montane forests at elevations from 835 to 1920 meters in the Cordillera Central and the Cordillera de Talamanca in Costa Rica and western Panamá (fig. 130). In Costa Rica, the species is known from both the Atlantic and the Pacific slopes of the aforementioned mountain ranges, but in Panamá, it has

been found only on the Pacific slopes in the extreme western part of the country.

See Appendix 1 for the locality records of the 113 specimens examined.

Hyla rivularis Taylor

Hyla rivularis Taylor, 1952c, p. 847 [holotype, K.U. No. 28197 from Isla Bonita, Heredia Province, Costa Rica; Richard C. Taylor and Edward H. Taylor collectors].

DIAGNOSIS: This small species has a tan, yellowish tan, or pale gray dorsum with darker markings that usually are irregularly longitudinal, but form transverse marks in some individuals. The thighs, upper arms, flanks, and venter are creamy yellow; the venter and flanks usually are heavily flecked with brown or black. This general coloration, plus the absence of white stripes on the lip and limbs or above the anus distinguish *rivularis* from all other Middle American hylids.

DESCRIPTION: This is a moderately small frog; males attain a maximum snout-vent length of 34.0 mm., and females reach 36.4 mm. In a sample of 25 males from the north slopes of Cerro Pando, Bocas del Toro Province, Panamá, the snout-vent length is 29.9 to 34.0 (mean, 32.3) mm.; the ratio of tibia length to snout-vent length is 0.443 to 0.490 (mean, 0.463); the ratio of foot length to snout-vent length is 0.400 to 0.460 (mean, 0.428); the ratio of head length to snout-vent length is 0.300 to 0.329 (mean, 0.313); the ratio of head width to snout-vent length is 0.311 to 0.333 (mean, 0.323), and the ratio of the diameter of the tympanum to that of the eye is 0.303 to 0.455 (mean, 0.367). In six females from the same locality, the snout-vent length is 34.4 to 36.4 (mean, 35.7) mm. The ratio of the diameter of the tympanum to that of the eye is 0.361 to 0.455 (mean, 0.409); there are no noticeable differences in other proportions between the males and the females. Although minor differences in size and proportions occur throughout the range, there does not seem to be any consistent geographic variation in these characters.

The head is as wide as the body and the top of the head is flat or slightly convex. In dorsal profile the snout is acutely rounded; in lateral profile the snout is acutely rounded anterodorsally and is inclined posteroventrally to the lip. The snout is moderately short; the

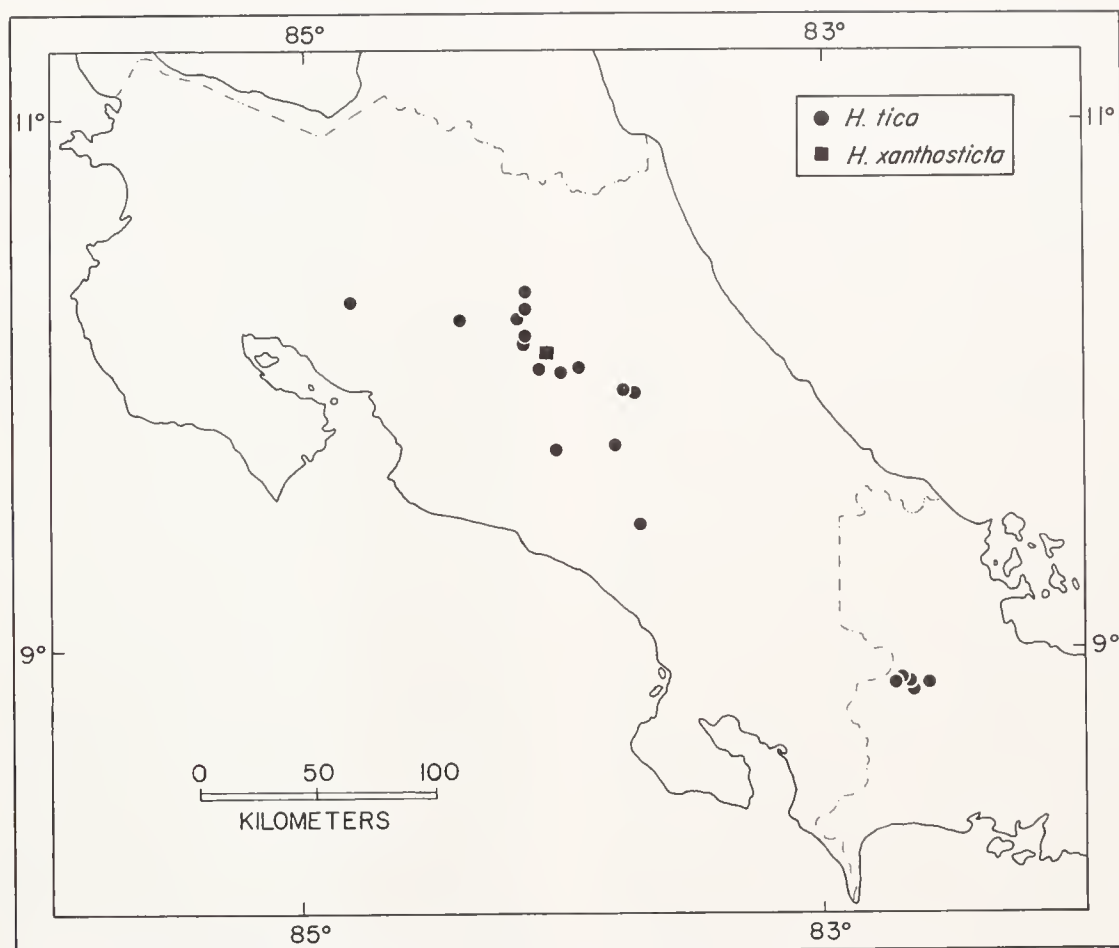


FIG. 130. Distribution of *Hyla tica* and *Hyla xanthosticta*.

nostrils are not noticeably protuberant and are situated about three-fourths the distance from the eyes to the tip of the snout. The canthus is strongly angular; the loreal region is noticeably concave, and the lips are moderately thick and barely flared. A thin dermal fold extends posteriorly from the posterior corner of the eye to a point above the insertion of the arm; the fold obscures the upper edge of the tympanum. If the tympanic ring is present at all, only the ventral part is evident. The rest of the tympanum is barely discernible beneath the skin. The tympanum is postero-ventral to the eye and separated from the eye by a distance equal to about two-thirds the diameter of the tympanum.

The arm is moderately short and robust; a brief axillary membrane is present. A row of

tubercles form a low dermal ridge along the ventrolateral edge of the forearm. A distinct transverse fold is present on the wrist. The fingers are short and broad and have large discs, the diameter of the disc on the third finger is usually slightly larger than the diameter of the tympanum. The subarticular tubercles are either bifid or completely divided in most specimens; in some individuals some tubercles are single, especially on the third finger. The supernumerary tubercles are large, conical, and rather broad; these tubercles are scattered irregularly on the basal segments of each digit and on the median digits are arranged in one or two rows. A rather small, bifid outer palmar tubercle is present. The prepollex is moderately enlarged; breeding males have a nuptial excrescence composed of

many spinules. The fingers are no more than one-third webbed (fig. 126B). The web is vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third finger; from the middle of the antepenultimate phalanx of the third, the web extends to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels overlap by about one-fifth the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. The tarsal fold is lacking. A thin, scalloped dermal fold extends from the heel along the outer edge of the foot to the base of the fifth toe. The inner metatarsal tubercle is ovoid, flat, and broadly visible from above. The outer metatarsal tubercle is small and conical. The toes are moderately short and robust; the discs are only slightly smaller than those on the fingers. The subarticular tubercles are moderately large, round, and subconical; the supernumerary tubercles are arranged in a single row on each digit and are nearly as large as the smaller subarticular tubercles. The toes are about two-thirds webbed (fig. 127B). The web extends from the base of the penultimate phalanx of the first to the base of the penultimate phalanx of the second toe, from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe. A narrow fringe extends along the outer edge of the fifth toe.

The anal opening is directed posteroventrally near the level of the upper edges of the thighs. No distinct anal sheath is present; the anal opening is surrounded, except dorsally, by moderately large tubercles. The skin on the chest, belly, and posteroventral proximal surfaces of the thighs is coarsely granular; elsewhere, the skin is smooth. A faint thoracic fold is present. The tongue is broadly cordiform, shallowly notched posteriorly and only barely free behind. In a sample of 25 males from the north slope of Cerro Pando, Bocas del Toro Province, Panamá, the total number of prevomerine teeth is four to eight (mean,

7.1), and in six females the number of prevomerine teeth is nine to 12 (mean, 10.8). There are two to six teeth on each of the small rounded prevomerine processes situated between the moderately small, ovoid inner nares. The vocal slits extend from the mid-lateral base of the tongue to the angle of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla rivularis* is pale yellowish tan with faintly darker dorsal markings (pl. 53, fig. 2). When active at night, the frogs usually are pale yellowish tan with the dorsal markings barely discernible. By day, the dorsum is olive-tan to yellowish tan with olive-brown to brown markings. The anterior and posterior of the thighs are pale olive-brown to yellowish brown. The belly is creamy yellow with dark brown or black flecks. The iris is bronze with fine black reticulations. The vocal sac is pale creamy yellow. The dorsal markings consist of a chevron-shaped interorbital bar and irregularly shaped markings on the back that usually form a longitudinal pattern, consisting of a pair of dark marks that may be discreet or interconnected. In some individuals, a median dark mark is present in the scapular region, and in some others there is a transverse dark mark above the anus. The dorsal surfaces of the thighs and shanks are colored like the dorsal surfaces of the body; in some specimens faint transverse bands are visible on the dorsal surfaces of the shanks. In many specimens, small dark brown flecks are present on the dorsal surfaces of the shanks and feet. A narrow creamy white line is present on the ventrolateral edge of the forearm; a white line extends from the heel to the base of the fifth toe. In approximately half of the specimens a short white anal stripe is present; in most of these, the tubercles bordering the anal opening also are white. The ventral surfaces of the hind legs are dull yellowish tan. In some individuals from throughout the range, but especially in western Panamá, bright metallic green flecks are scattered on the dorsum. All individuals have some dark spots on the venter; in some specimens, the spots are numerous and rather large; in others, they are few in number and small. In many individuals the dots are present also on the ventral sur-

faces of the thighs and on the throat, but in approximately half of the specimens the throat lacks dark spots.

In preserved specimens, the dorsal ground color varies from tan to gray or pale reddish brown; the dorsal markings are dark brown or dark gray. The venter is creamy white with brownish black spots. The anterior and posterior surfaces of the thighs are yellowish tan to grayish brown.

TADPOLES: The sizes and proportions of tadpoles from Cinchona, Alajuela Province, Costa Rica are given in table 32. A typical tadpole in developmental stage 36 from the south fork of the Río Las Vueltas, Heredia Province, Costa Rica, has a body length of 12.9 mm. and a total length of 39.7 mm. The body is slightly wider than deep. In dorsal profile the snout is broadly truncate; in lateral profile it is rounded. The nostrils are small, situated dorsolaterally, directed anteriorly, and are at a point about one-fourth the distance from the eyes to the tip of the snout. The eyes are moderately small and directed dorsolaterally. The spiracle is sinistral and is situated about equidistant from the eye to the posteroventral edge of the body. The anal tube is short and median. The caudal musculature is heavy and terminates near the tip of the caudal fin, which is bluntly rounded terminally. At mid-length of the tail the musculature is about as deep as either the dorsal or ventral fins; the dorsal fin barely extends onto the body (fig. 128B).

The mouth is large and ventral; when it is fully opened it is visible anteriorly and laterally from above. The lips are folded laterally. The lips are completely bordered by three rows of moderately large peg-like papillae; one or two rows of small papillae are also present on the edge of the lower lip. A few large papillae are present laterally in the fold of the lip. The upper beak is bow-shaped with long, slender, turned lateral processes. The lower beak is moderately robust and V-shaped; both beaks bear fine serrations. There are two upper and three lower rows of teeth; usually all rows are complete. The upper rows are equal in length and only slightly longer than the lower rows (fig. 129B).

The body is dull brown with golden flecks, especially laterally. The caudal musculature is creamy tan with dark brown blotches dorsally and brown or black flecks laterally. The caudal fins are transparent, except for scattered brown flecks. The iris is greenish bronze. In preservative, the body is dark brown; the caudal musculature is creamy white with brown flecks laterally and ventrally and brown markings dorsally. The dorsal markings tend to form broad transverse bars, separated by creamy white interspaces.

The tadpoles described here agree with the description of the species given by Starrett (1960a).

MATING CALL: The call of *Hyla rivularis* consists of a series of short, high-pitched, cricket-like notes. Each note contains three

TABLE 32
Sizes and Proportions of Tadpoles of *Hyla rivularis*
from Cinchona, Alajuela Province, Costa Rica.
(Means Are Given in Parentheses; Each Sample Contains Ten Specimens.)

Developmental Stage	Body Length	Tail Length	Total Length	Body/Tail
25	5.7-10.6 (9.2)	11.1-20.5 (18.0)	16.8-31.0 (27.3)	0.49-0.54 (0.511)
28	10.8-12.0 (11.5)	21.0-23.8 (22.6)	31.8-35.8 (34.1)	0.47-0.52 (0.508)
31	11.0-12.9 (12.0)	21.5-26.1 (24.5)	32.5-38.9 (36.5)	0.46-0.51 (0.489)
37	12.2-13.2 (12.7)	26.0-28.1 (26.9)	38.8-40.7 (39.6)	0.44-0.49 (0.472)
41	13.0-14.8 (14.0)	26.0-28.5 (27.4)	39.0-43.3 (41.3)	0.49-0.53 (0.510)

pulses; the notes have a dominant frequency of about 2420 cycles per second. Each call group consists of 12 to 137 notes and has a duration of five to 66 seconds; call groups are repeated at intervals of about 10 to 70 seconds (pl. 19, fig. 3; table 31).

NATURAL HISTORY: *Hyla rivularis* lives in cloud forests and breeds in clear, swift mountain streams. Males have been heard calling nearly every month of the year; probably due to equable climatic conditions in the cloud forests, this species breeds throughout the year. This suggestion is enhanced by the evidence of finding tadpoles in various stages of development throughout most of the year. Males call from herbs and low bushes at the edge of, or overhanging, fast-moving water. Usually the calling frogs are well hidden in

the foliage; it is infrequent that a calling male is observed on a conspicuous perch.

The tadpoles are usually found in pools in the rocky streams. The tadpoles adhere to the top and sides of large rocks in the pool. When the tadpoles are disturbed, they either move a short distance over the surface of the rock or seek refuge under rocks at the bottom of the pool.

Three recently metamorphosed young from Chinchona, Alajuela Province, Costa Rica, have snout-vent lengths of 13.8, 14.8, and 15.0 mm. These small specimens were pale tan above and lacked dorsal dark markings, although one individual had numerous green flecks on the back. The venter was immaculate yellow.

REMARKS: This species is abundant in the

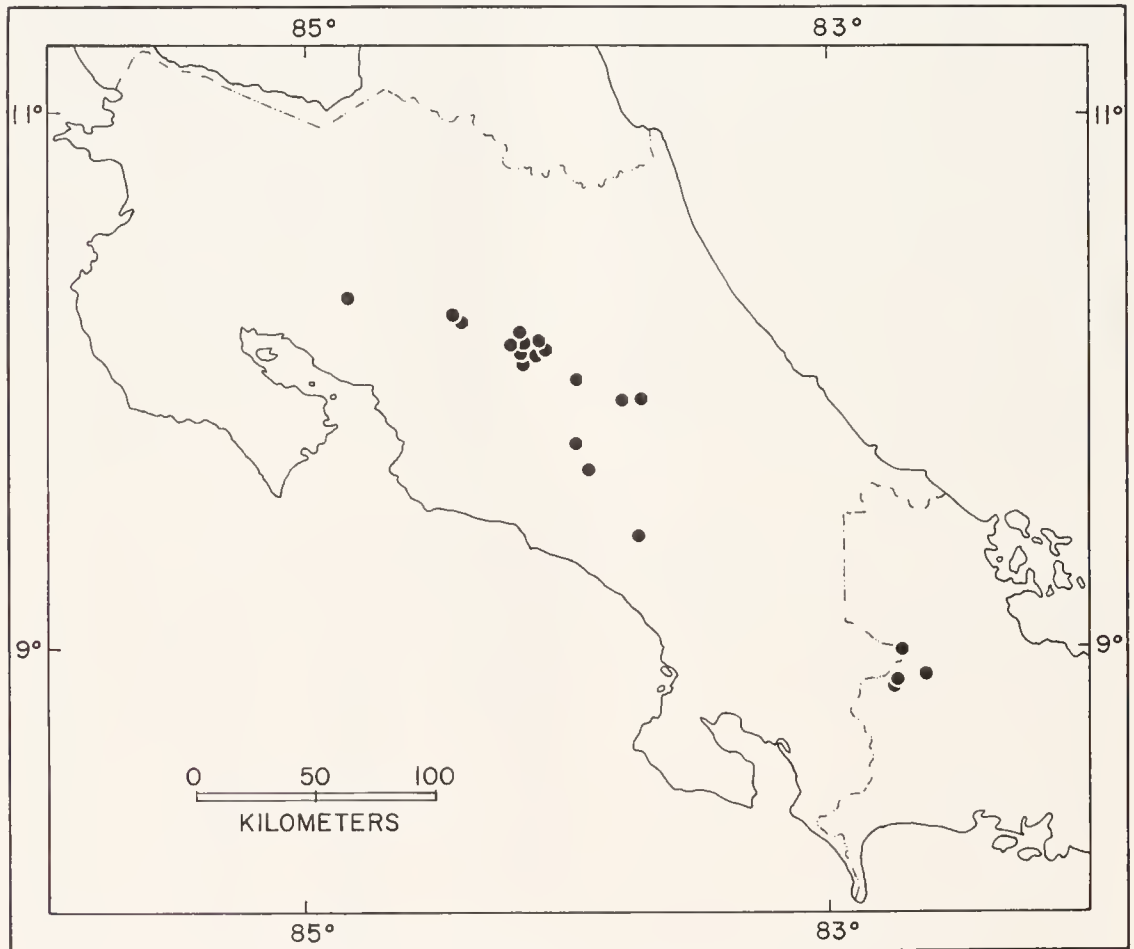


FIG. 131. Distribution of *Hyla rivularis*.

high mountains of Costa Rica and western Panamá; along mountain streams in these mountains, *Hyla rivularis* occurs sympatrically with *Hyla pictipes* at higher elevations and *Hyla tica* and *uranochroa* at lower elevations. At elevations below 1500 meters, *Hyla rivularis* apparently is replaced by *Hyla debilis*.

ETYMOLOGY: The trivial name is Latin, *rivularis*, meaning "of a stream." The name was applied in reference to the stream-side habitat of this small frog.

DISTRIBUTION: *Hyla rivularis* inhabits cloud forests at elevations of 1280 and 2840 meters on both the Atlantic and Pacific slopes of the Cordillera Central, Costa Rica, and the Cordillera Talamanca in Costa Rica, and western Panamá (fig. 131).

See Appendix 1 for the locality records of the 303 specimens examined.

Hyla debilis Taylor

Hyla debilis Taylor, 1952c, p. 880 [holotype, K.U. No. 28184 from Isla Bonita, Heredia Province, Costa Rica; Richard C. Taylor and Edward H. Taylor collectors].

DIAGNOSIS: This small species has an olive-green dorsum with small black flecks and a uniformly white belly; the flanks are white with small brown flecks. The thighs are olive-green dorsally and yellow posteriorly. A narrow dark brown canthal stripe is bordered above by a bronzy tan stripe. A narrow white labial stripe usually is interrupted and expanded to form a spot below the eye. This species can be distinguished from *xanthosticta* by having yellow thighs and white flanks, instead of having both dark brown with yellow spots. Furthermore, *xanthosticta* has narrow white stripes on the forearm and tarsus and above the anus, and a continuous labial stripe. Superficially, *Hyla debilis* resembles *Hyla rufoculis* and *uranochroa*, both of which differ from *debilis* by having a white lateral stripe, white anal stripe, and red eye. The only other Middle American hylid that could be confused with *debilis* is *Ptychohyla schmidtorum chamulae*. That species has dull yellow thighs, a broad labial stripe which is continuous across the base of the arm to a stripe on the flank, and ventrolateral glands in breeding males.

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 29.5

mm., and females reach 31.6 mm. In a sample of nine males from an elevation of 1450 meters on the north slope of Cerro Pando, Bocas del Toro Province, Panamá, the snout-vent length is 26.1 to 29.5 (mean, 27.5) mm.; the ratio of tibia length to snout-vent length is 0.461 to 0.515 (mean, 0.490); the ratio of foot length to snout-vent length is 0.390 to 0.462 (mean, 0.426); the ratio of head length to snout-vent length is 0.295 to 0.323 (mean, 0.310); the ratio of head width to snout-vent length is 0.284 to 0.316 (mean, 0.303), and the ratio of the diameter of the tympanum to that of the eye is 0.452 to 0.593 (mean, 0.534). Five females from the same locality have snout-vent lengths of 26.8 to 31.6 (mean, 29.9) mm. The females do not differ from the males in any of the proportions. Eleven males from Tapantí, Cartago Province, Costa Rica have snout-vent lengths of 24.9 to 26.8 (mean, 25.8) mm.; a single specimen from that locality has a snout-vent length of 28.3 mm. Although the Costa Rican specimens are slightly smaller than those from Panamá, there are no significant differences in the proportions.

The head is as wide as the body; the top of the head is flat or slightly convex. In dorsal profile the snout is acutely rounded; in lateral profile it is rounded above and inclined posteroventrally to the lips. The snout is moderately long; the nostrils are barely protuberant and are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is angular; the loreal region is noticeably concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the posterior corner of the eye and curves along the upper edge of the tympanum and thence downward to the anterior edge of the insertion of the arm. The fold covers the upper edge of the tympanum, which otherwise is distinct. The tympanum is situated posterior, and slightly ventral to the eye and is separated from the eye by a distance nearly equal to the diameter of the tympanum.

The arm is moderately short and robust. An abbreviated axillary membrane is present. A row of low tubercles forms a dermal ridge along the ventrolateral edge of the forearm; a distinct transverse dermal fold is present on

the wrist. The fingers are relatively short and broad and bear relatively small discs; the disc on the third finger is about two-thirds the diameter of the tympanum. The subarticular tubercles are moderately large and round; the distal tubercle beneath the fourth finger is usually bifid; the distal one on the third finger is bifid in about one-third of the specimens. The supernumerary tubercles are small and low. A bifid or tripartite palmar tubercle is weakly defined. The prepollex is moderately enlarged and in breeding males bear a horny nuptial excrescence composed of many small spinules. The hands are about one-third webbed (fig. 126C). The webbing is vestigial between the first and second fingers, extends from the base of the penultimate phalanx of the first to the base of the antepenultimate phalanx of the second, and from the middle of the antepenultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third finger. The hind limbs are moderately short and robust; the adpressed heels overlap by about one-fifth the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. The tarsal fold is absent. A row of low tubercles forms an indistinct dermal fold on the outer edge of the tarsus. The inner metatarsal tubercle is low, flat, ovoid, and barely visible from above; the outer metatarsal tubercle is a minute cone-shaped bump. The toes are moderately long and slender and bear discs that are about the same size as those on the fingers. The subarticular tubercles are moderately small, round, and conical. The subarticular tubercles are usually absent on the distal segments of the toes and only weakly defined, if at all, on the proximal segments. The toes are about two-thirds webbed (fig. 127C). The webbing extends from the base of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second toe, from the middle of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and onto the distal end of the penultimate phalanx of the fifth toe. A narrow dermal fringe extends along the outer edge of the fifth toe.

The anal opening is directed posteroventrally at the level of the middle of the thighs. A short anal sheath is present; the area below the anal opening is covered with large tubercles. The skin on the belly and the proximal parts of the posteroventral surfaces of the thighs is strongly granular. Elsewhere the skin is nearly smooth. A weak thoracic fold is present. The tongue is broadly cordiform, barely notched posteriorly and only slightly free behind. The denticulous processes of the prevomers are small, elliptical structures lying between the posterior borders of the ovoid choanae. In males, two or three teeth are present on each prevomerine ridge; all females have three teeth on the ridge. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla debilis* is brown with green and darker brown flecks on the dorsum (pl. 53, fig. 3). Usually the side of the head and flanks are dull green, and the dorsal surfaces of the limbs, third and fourth fingers, and fourth and fifth toes are brown. The groin, anterior and posterior surfaces of thighs, ventral surfaces of hind limbs, and dorsal surfaces of the first three toes are deep yellow. The ventral surfaces of the forearm and dorsal surfaces of the first two fingers lack pigment. One or more labial spots, the throat, and belly are white. The anal tubercles, the stripe on the outer edge of the tarsus and fifth toe, and the stripe on the outer edge of the forearm and the fourth finger are creamy white. The iris is dull coppery bronze. The palpebrum is clear above but faintly reticulated with green below.

In preservative, the dorsum is dull gray or brown, with or without small darker flecks. The anterior and posterior surfaces of the thighs and groin are creamy tan. The venter is creamy white.

All specimens have a distinct white spot on the lip below the eye. Another, slightly smaller spot, is present on the upper lip midway between the eye and the nostril; another spot is usually present on the tip of the upper lip. In many specimens, this is confluent with the lateral spot. In most specimens there is a definite line of demarcation between the dark

dorsal pigment and the pale color on the posterior surfaces of the thighs, but in some individuals the edge of the dorsal dark color is scalloped, interrupted dorsally by extensions of the yellow on the posterior surfaces of the thighs, or scattered as discreet brown spots on the posterior surfaces of the thighs. Some males when calling at night were pale brown above with metallic green flecks, and the chin and belly were pale lemon yellow. One individual was uniform olive-tan above.

TADPOLES: In a series of ten tadpoles in developmental stage 25 from an elevation of 1450 meters on the north slope of Cerro Pando, Bocas del Toro Province, Panamá, the body length is 6.3 to 8.0 (mean, 7.2) mm.; the tail length is 12.5 to 15.4 (mean, 14.0) mm., and the total length is 19.0 to 23.4 (mean, 21.3) mm. Ten tadpoles in developmental stage 28 from the same locality have body lengths of 9.4 to 13.7 (mean, 11.6) mm., tail lengths of 17.1 to 29.3 (mean, 23.3) mm., and total lengths of 26.5 to 43.0 (mean, 34.9) mm. A large tadpole in developmental stage 28 has a body length of 13.7 mm. and a total length of 43.0 mm. The body is slightly depressed, barely wider than deep. In dorsal profile the snout is bluntly rounded; in lateral profile it is more acutely rounded. The eyes are small, widely separated, and directed dorsolaterally. The nostrils are situated dorsolaterally at a point about equidistant between the eyes and the tip of the snout. The spiracle is sinistral and situated on the midline at a point midway between the eye and the posterior edge of the body. The anal tube is short and dextral. The tail is long, low, and blunt terminally. The caudal musculature is robust; at midlength of the tail, the depth of the musculature is equal to the depth of either fin. The dorsal fin does not extend onto the body (fig. 128C).

The mouth is large and ventral in position. The lips are deeply folded laterally. Two or three rows of moderately large, blunt papillae border the lips; numerous papillae are present in the lateral fold. The beaks are robust; the upper beak forms a broad arch, and the lower beak is broadly V-shaped. Both beaks bear moderately long, fine serrations. There are two upper and three lower rows of teeth. In all tadpoles, the second upper row is inter-

rupted medially, whereas in approximately half of the specimens the first is interrupted and in others it is complete. The second upper row is slightly shorter than the first; the three lower rows are complete, approximately equal in length, and only slightly shorter than the second upper row (fig. 129C).

Dorsally the body is mottled dark brown and tan; this coloration extends onto the side of the body where some metallic gold flecking is present. The venter is dark brown except midventrally, where it is gray. The caudal musculature is tan with small brownish gray flecks and dark brown spots. The caudal fins are unpigmented except for a few brown spots and posteriorly a suffusion of gray flecks. The iris is a golden color with gray peripherally. In preservative, the anterior part of the body is dark brown; posteriorly the body is tan. The caudal musculature is creamy white with dark brown spots, which tend to form a longitudinal line along the dorsolateral edge of the caudal musculature.

MATING CALL: The mating call of *Hyla debilis* consists of a series of extremely weak "cricket-like" chirps. There are five to seven notes in each call group which has a duration of 0.10 to 0.16 of a second. There is only a single pulse per call, and the dominant frequency is at about 5235 cycles per second (table 31; pl. 21, fig. 2).

NATURAL HISTORY: The limited information on *Hyla debilis* indicates that this species is an inhabitant of lower reaches of cloud forests, where it breeds in mountain streams. Taylor (1952c) reported that the type and paratype were collected at Isla Bonita, Heredia Province, Costa Rica, on August 1, 1947. Norman Scott and J. M. Savage obtained this species at Tapantí, Cartago Province, Costa Rica, on September 27 and December 19, 1963. I collected *Hyla debilis* on several dates in May on the north slope of Cerro Pando, Bocas del Toro Province, Panamá. Despite the intensive field work by several herpetologists in the area around Isla Bonita and at Tapantí, the species has not been found again at either of these localities. Since there are several stream-breeding frogs at these localities it is conceivable that the species has been present there at the time

when the collectors visited, but because of the weak voice it is not easily found.

On the north slope of Cerro Pando, males of *Hyla debilis* called from concealed sites within dense vegetation at the edge of, or overhanging, small mountain streams. Females were found on bushes near the streams, except one which was sleeping on the leaf of a tree approximately 300 meters from the nearest stream.

The tadpoles were found adhering to the sides and tops of rocks in the bottom of the pool in a small, rocky, gravel-bottomed stream. Two tadpoles were raised to metamorphosis at which time they had snout-vent lengths of 12.7 and 13.1 mm. Another juvenile having a snout-vent length of 17.8 mm. was found on low vegetation near a stream. The juveniles were colored like the adults, except that a creamy canthal stripe was apparent, and the loreal region was pale green. Furthermore, one of the juveniles had a distinct olive tint to the brown dorsal coloration.

REMARKS: *Hyla debilis* seems to replace *Hyla rivularis*, which is known from higher elevations. The two frogs are extremely similar in their mating calls, general morphology, and breeding behavior. Likewise, the tadpoles occupy the same microhabitat within the stream.

A specimen (U.M.M.Z. No. 69496) from Boquete, Chiriquí Province, Panamá, is tentatively assigned to this species. Most of the pigment is faded, and identification can not be certain.

ETYMOLOGY: The specific name is Latin, *debilis*, meaning weak, in reference to the voice of this species.

DISTRIBUTION: *Hyla debilis* is known from cloud forests from elevations of 910 to 1450 meters on the Caribbean slopes of the Cordillera Central in Costa Rica and the Cordillera Talamanca in Costa Rica and western Panamá. If the specimen from Boquete is correctly identified, this specimen represents the only record for the species on the Pacific slope (fig. 132).

See Appendix 1 for the locality records of the 40 specimens examined.

Hyla xanthosticta Duellman

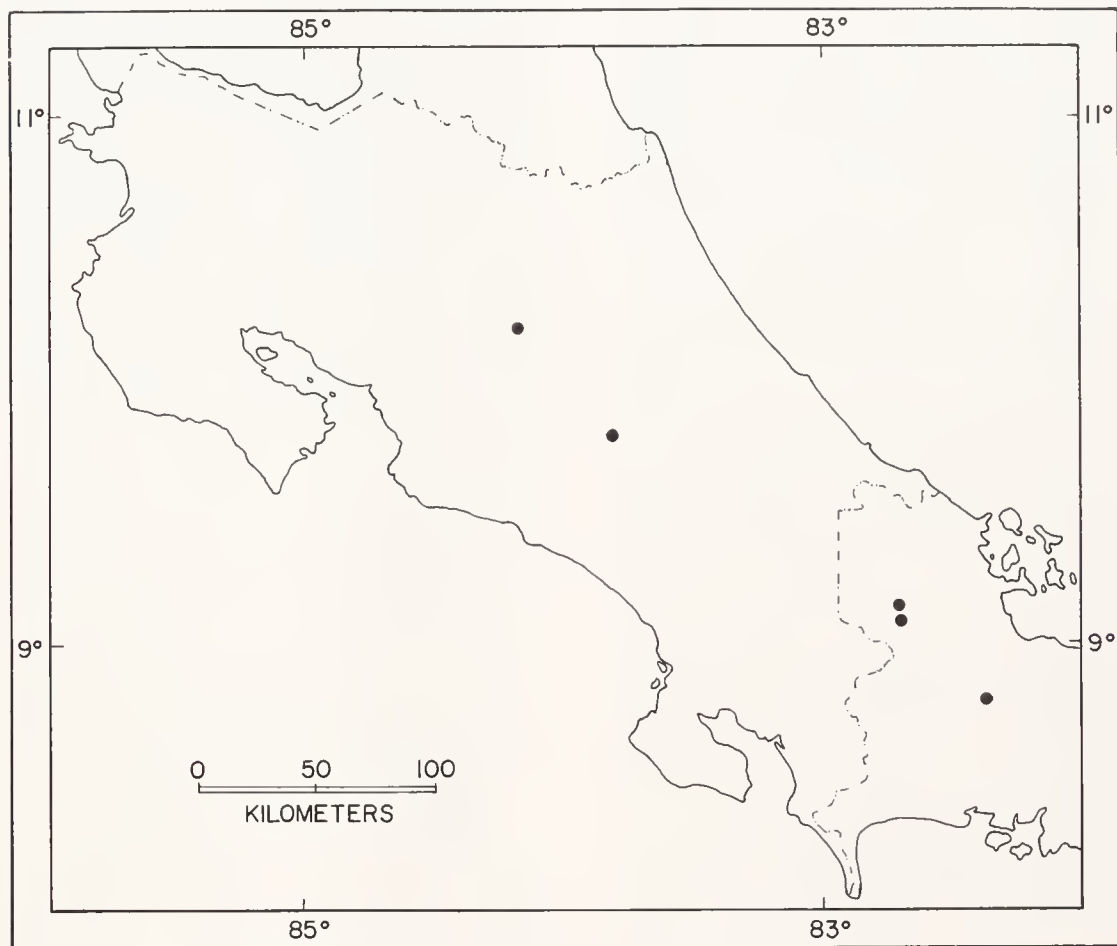
Hyla xanthosticta Duellman, 1968a, p. 562 [holotype, K.U. No. 103772 from the south fork of the Río

Las Vueltas, on the south slope of Volcán Barba, near the northwest base of Cerro Chonpipe, Heredia Province, Costa Rica, 2100 meters; John D. Lynch collector].

DIAGNOSIS: This member of the *Hyla rivularis* group has a uniform green dorsum and unmarked throat and belly; the flanks and thighs are dark brown with large bright yellow spots (white in preservative). A broad bronze-tan canthal stripe is present. This combination of characters distinguishes *xanthosticta* from all known Middle American hylids. *Hyla debilis* possesses the canthal stripe but has creamy white flanks and yellow posterior surfaces of the thighs. Furthermore, *xanthosticta* has a narrow continuous white labial stripe; the labial stripe in *debilis* usually is interrupted and expanded below the eye. Female *Hyla pictipes* have small yellow spots on dark brown or black flanks and thighs, but lack the white stripes on the lips, forearms, tarsi, and above the anus that are present in *xanthosticta*. Furthermore, *pictipes* has a spotted venter. The Mexican *Hyla euphobiacea* has brown thighs with small yellow spots, but in that species the dorsum is green with brown markings and broad brown canthal and postorbital stripes are present.

DESCRIPTION: This species is known from a single specimen, a female, having a snout-vent length of 29.3 mm.; the ratio of the tibia length to the snout-vent length is 0.553; the ratio of foot length to snout-vent length is 0.481; the ratio of head length to snout-vent length is 0.341; the ratio of head width to snout-vent length is 0.352, and the ratio of the diameter of the tympanum to that of the eye is 0.500.

The head is as wide as the body; the top of the head is convex. In dorsal profile the snout is narrow and truncate; in lateral profile it is truncate, slightly inclined posteroven- trally. The snout is moderately long. The nostrils are slightly protuberant, directed laterally, and situated at about four-fifths the distance from the eye to the tip of the snout. The canthus is angular; the loreal region is barely concave, and the lips are thick and barely flared. A moderately heavy dermal fold extends from the posterior corner of the eye and curves above the tympanum downward to the anterior edge of the insertion of the arm.

FIG. 132. Distribution of *Hyla debilis*.

The fold obscures the upper edge of the tympanum, which otherwise is barely distinct. The tympanum is situated posteroventrally to the eye and is separated from the eye by a distance equal to twice the diameter of the tympanum.

The arms are moderately long and slender; there is no axillary membrane. A thin, scalloped dermal fold is present on the ventrolateral edge of the forearm; a thin transverse dermal fold is present on the wrist. The fingers are long and rather slender. The discs are moderately large; that on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large; the distal tubercle on the third finger is broad and flat; the distal tubercle on the fourth finger is

strongly bifid. Supernumerary tubercles are large, round, closely spaced, and irregular on the proximal segments of the digits. The prepollex is moderately enlarged. The fingers are about one-fourth webbed (fig. 126D). The web is lacking between the first and second fingers and vestigial between the second and third. The web extends from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and slender; the heels overlap by about one-third the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A thin transverse dermal fold is present on the heel and a scalloped dermal fold extends along the outer edge of

the tarsus. The tarsal fold is lacking. The inner metatarsal tubercle is large, flat, elliptical, and visible from above. The outer metatarsal tubercle is small and subconical. The toes are long and slender; the discs are slightly smaller than those on the fingers. The sub-articular tubercles are large, round, and subconical; the supernumerary tubercles are few in number and are scattered on the proximal segments of the digits. The toes are about two-thirds webbed (fig. 127D). The web extends from the middle of the penultimate phalanx of the first toe to the middle of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs; it is bordered below by large tubercles. There is no anal sheath. The skin is smooth on the dorsum except for small scattered tubercles; the skin on the belly and posteroventral surfaces of the thighs is granular. The tongue is round, emarginate, and barely free behind. There are five prevomerine teeth on each side, situated on large ovoid elevations at a level of the posterior edges of the small, round choanae.

The general coloration of *Hyla xanthosticta* is green with brown flanks and thighs with large yellow spots (pl. 53, fig. 4). The green dorsum is palest on the sides of the head. The dorsal surfaces of the thighs are tan. The flanks, anterior and posterior surfaces of the thighs, and the inner surfaces of the tarsi are brown with bright yellow spots. A broad bronze-tan (reddish copper at night) canthal stripe is present. The throat and belly are pale yellow; the ventral surfaces of the limbs are dull, dark yellow. A large, bright yellow spot is present on the anteroventral surface of each thigh. Bright yellow tubercles are present on the median part of the thighs. The anal area is dark brown with a white stripe above and a yellow stripe below. There is a white stripe on the outer edge of the forearm, one on the outer edge of the tarsus, and another on the edge of the upper lip.

The iris is a golden color with fine black reticulations and faint reddish suffusion medially. The palpebral membrane is clear.

In preservative, the dorsum is dark purplish brown and brown on the limbs. The first three fingers and first three toes are creamy yellow and the other digits are brown. The flanks are dark brown with white spots; the anterior and posterior surfaces of the thighs and inner surfaces are brown with cream-colored spots. The stripes on the edge of the upper lip, ventrolateral edge of the forearm, outer edge of the tarsus, and above the anus are white. The chin and throat are white, and the belly and ventral surfaces of the limbs are creamy white.

TADPOLES: The tadpoles of this species have not been collected. Presumably, they develop in mountain streams.

MATING CALL: The call of *Hyla xanthosticta* is unknown.

NATURAL HISTORY: The only known specimen of *Hyla xanthosticta* was perched at night on a leaf about 1 meter above the ground. The frog was found in humid upper montane forest characterized by large oaks supporting many bromeliads and heavy growths of mosses.

REMARKS: On the basis of external morphological characters and partial dissection of the skull, it is possible to ally *Hyla xanthosticta* with the *Hyla rivularis* group. At the type locality on Volcán Barba, Heredia Province, Costa Rica, *Hyla xanthosticta* occurs sympatrically with *Hyla rivularis* and *Hyla pictipes*.

ETYMOLOGY: The specific name is derived from the Greek *xanthos* meaning yellow and the Greek *stiktos* meaning spotted, and alludes to the diagnostic yellow spots on the flanks and thighs.

DISTRIBUTION: *Hyla xanthosticta* is known only from an elevation of 2100 meters on the south slope of Volcán Barba, Heredia Province, Costa Rica (fig. 130).

See Appendix 1 for the locality record for the one specimen examined.

The *Hyla pictipes* Group

DEFINITION: The one species in this group is a moderately small, stream-breeding frog; males attain a maximum snout-vent length of 39 mm. and females, 45 mm. The dorsum is

green or mottled dull green and black. The fingers are about one-fourth webbed, and the toes are about three-fourths webbed. Dermal appendages and fringes are lacking. Males have a single, median, subgular vocal sac and a horny nuptial excrescence on the pollex. The cranial elements are moderately ossified; a medium-sized frontoparietal fontanelle is present. The sphenethmoid is rather short; the nasals are in partial bony contact with the sphenethmoid and lack maxillary processes. The quadratojugal is absent. The pterygoid lacks a bony connection with the prootic. The anterior arm of the squamosal is short and blunt. Prevomerine teeth are present (fig. 133). The tadpoles have a long terminally rounded tail and a large, ventral mouth with two upper and three lower rows of teeth. The mating call consists of a single, pulsed, low-pitched note. The haploid number of chromosomes is 12.

COMPOSITION: *Hyla pictipes* is the sole

member of the group; 143 preserved specimens, five skeletons, and nine lots of tadpoles have been examined.

COMMENTS: Starrett (1966) included *Hyla debilis*, *rivularis*, and *pictipes* in the *Hyla pictipes* group. The reasons for segregating *pictipes* from the other species are presented in the account of the *Hyla rivularis* group.

Hyla pictipes Cope

Hyla punctariola pictipes Cope, 1876, p. 106 [syn-types, U.S.N.M. Nos. 30631 and 30652 from Pico Blanco, Limón Province, Costa Rica; William M. Gabb collector].

Hyla punctariola moesta Cope, 1876, p. 106 [holotype, U.S.N.M. No. 20660 from Pico Blanco, Limón Province, Costa Rica; William M. Gabb collector].

Hyla punctariola monticola Cope, 1876, p. 106 [holotype, U.S.N.M. No. 30661 from Pico Blanco, Limón Province, Costa Rica; William M. Gabb collector].

Hyla punctariola: Boulenger, 1882a, p. 401 [part].

Hyla moesta: Taylor, 1952c, p. 855.

Hyla monticola: Taylor, 1952c, p. 855.

Hyla pictipes: Taylor, 1952c, p. 878. Starrett, 1966, p. 17 [synonymized *Hyla punctariola moesta* Cope, 1876, and *Hyla punctariola monticola* Cope, 1876, with *Hyla pictipes*].

DIAGNOSIS: *Hyla pictipes* differs from all other Middle American hylids by having a mottled green and black dorsum in males and uniform green dorsum in females, dark brown or black flanks and posterior surfaces of the thighs with small creamy white or yellow spots, an angular snout in lateral profile, the fingers only one-third webbed, and dark spots on the venter. *Hyla tica* is similar in general appearance, but has a rounded snout, and a larger tympanum; the average ratio of the diameter of the tympanum to that of the eye in *pictipes* is 0.377 and in *tica*, 0.517. *Hyla xanthosticta* superficially resembles females of *pictipes*, but the former has larger yellow spots on the flanks and thighs and has a bronze-tan canthal stripe and white stripes on the outer edges of the forearms and tarsi, on the edge of the upper lip, and above the anus; these stripes are usually absent in *pictipes* (labial stripe present in some specimens).

DESCRIPTION: Males of this moderate-sized species attain a maximum snout-vent length of 39.0 mm., and females reach 45.1 mm. In a sample of 25 males from the Río Poasito on Volcán Poas, Alajuela Province, Costa Rica,

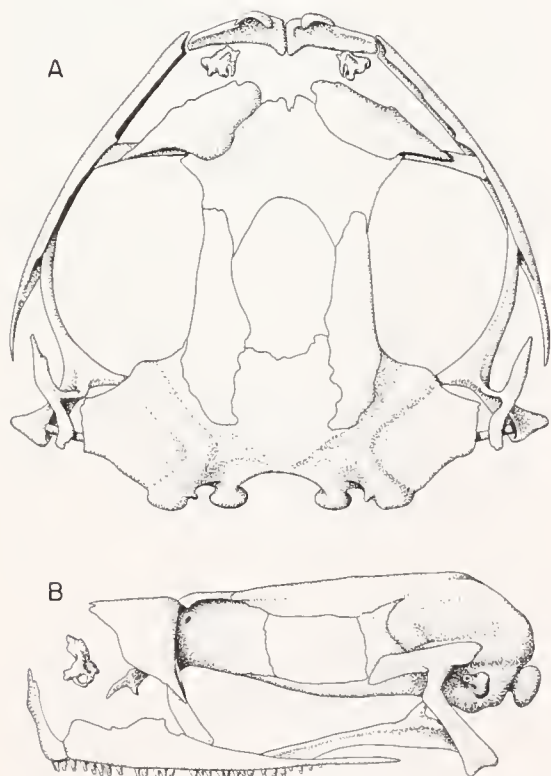


FIG. 133. Dorsal (A) and lateral (B) views of the skull of *Hyla pictipes*, K.U. No. 68314. $\times 5$.

the snout-vent length is 31.8 to 37.6 (mean, 34.8) mm.; the ratio of tibia length to snout-vent length is 0.478 to 0.540 (mean, 0.505); the ratio of foot length to snout-vent length is 0.421 to 0.484 (mean, 0.457); the ratio of head length to snout-vent length is 0.298 to 0.345 (mean, 0.315); the ratio of head width to snout-vent length is 0.306 to 0.355 (mean, 0.326), and the ratio of the diameter of the tympanum to that of the eye is 0.289 to 0.514 (mean, 0.377). Six females from the same locality have snout-vent lengths of 40.9 to 44.6 (mean, 42.7) mm. They do not differ significantly from the males in proportions, except that the tympanum is slightly larger; the ratio of the diameter of the tympanum to that of the eye is 0.295 to 0.487 (mean, 0.405).

The body is robust; the head is not quite as wide as the body. The top of the head is slightly convex. In dorsal profile, the snout is acutely rounded; in lateral profile, it is rounded above and slightly inclined posteroventrally. The snout is moderately short; the nostrils are slightly protuberant and are situated approximately two-thirds the distance from the eyes to the tip of the snout. The canthus is rounded, but distinct; the loreal region is nearly flat and continuous with the thick and barely flared lips. A moderately heavy dermal fold extends posteriorly from the posterior corner of the eye and curves above the tympanum to a point above the insertion of the arm. The fold covers the upper edge of the tympanum, which otherwise is barely distinct beneath the skin. The tympanum is located posteroventral to the eye and is separated from the eye by a distance equal to about half again the diameter of the tympanum.

The arm is moderately long and slender; there is no axillary membrane. A row of low tubercles is present along the ventrolateral edge of the forearm, but these do not form a dermal ridge. A heavy transverse dermal fold is present on the wrist. The fingers are relatively long, but robust, and bear large discs; the disc on the third finger is half again as broad as the diameter of the tympanum. The subarticular tubercles are large and subconical; the distal tubercle on the fourth finger is divided or bifid in all specimens. The supernumerary tubercles are moderately large, distinct, and subconical. They are arranged in a

single row on the proximal segments on the second and third fingers and in one or two rows on the proximal segment of the fourth finger. The outer palmar tubercle is low, flat, and indistinct in most specimens; in many individuals it is tripartite. The prepollex is greatly enlarged, and in breeding males it bears a horny nuptial excrescence. The hands are about one-fourth webbed (fig. 134A). The webbing is vestigial between the first and second fingers; it extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third finger and from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the adpressed heels overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the middle of the eye. There is no tarsal fold. The inner metatarsal tubercle is low, flat, elliptical, and visible from above. The outer metatarsal tubercle is small and subconical. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the hands. The subarticular tubercles are moderately large and subconical. The supernumerary tubercles are small, conical, and present only on the proximal segments of the toes. The toes are about three-fourths webbed (fig. 134B). The webbing extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the base of the disc of the fifth toe. A thin dermal fringe extends from the inner metatarsal tubercle to the base of the disc of the first toe; another dermal fringe is present on the lateral edge of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs. The opening is covered by a short, thick anal sheath. The skin on the dorsal surfaces of the body and limbs and on the ventral surfaces of the shanks is smooth; that on the ventral surfaces of the forelimbs and thighs and on the throat and belly is granular. The tongue is ovoid,

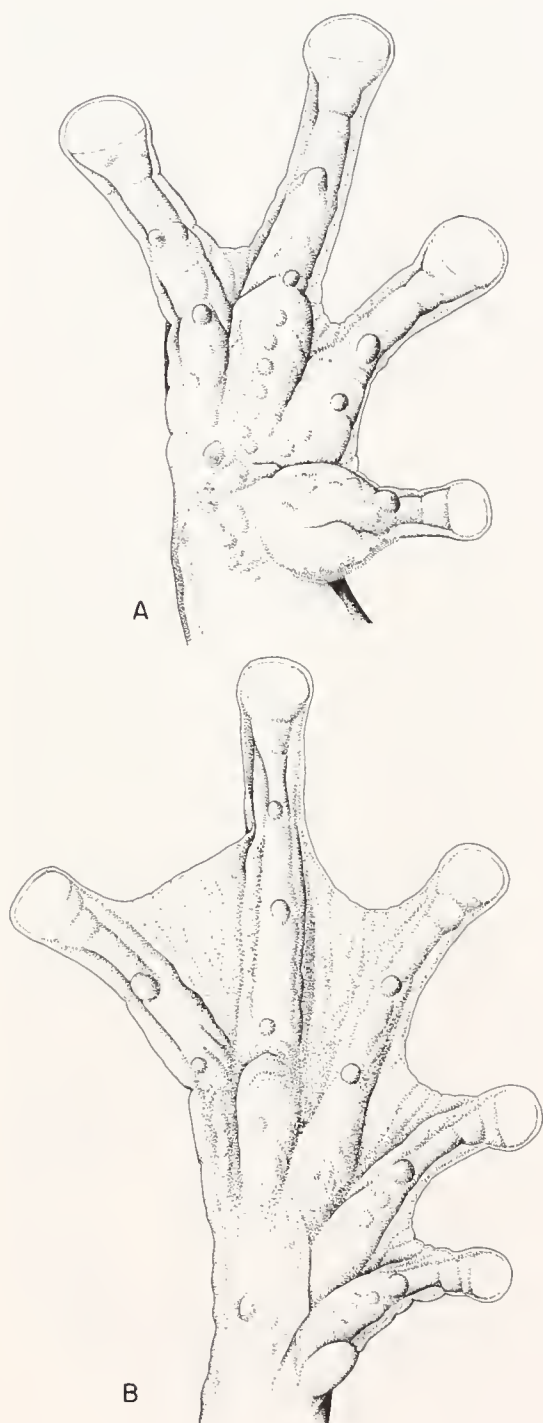


FIG. 134. Hand (A) and foot (B) of *Hyla pictipes*, K.U. No. 103694. $\times 5$.

nearly as broad as long. In some specimens, it is emarginate, but in most it is shallowly notched either anteriorly, posteriorly, or both. The dentigerous processes of the prevomers are moderately large and elliptical; they are situated between the posterior borders of the relatively ovoid choanae. Males have three to six teeth on each prevomerine process and have a total of six to 12 (mean, 9.0) prevomerine teeth. Females have five to eight teeth on each process and a total of 11 to 15 (mean, 12.7) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and barely distensible.

The general coloration of *Hyla pictipes* is dull green with dark brown or black mottling dorsally in males or fairly uniform green dorsally in females (pl. 53, figs. 5 and 6). The dorsal ground color in males varies from pale green to dull olive-green or olive-tan with darker olive-brown, dark brown, or black mottling. In most individuals, the mottling covers a greater part of the dorsum than does the ground color. The upper surfaces of the limbs are colored like the body; there are no distinct bars on the limbs. The loreal region is usually a dull pale green. The anterior and posterior surfaces of the thighs and the flanks are dark brown with small, bright yellow spots. The ventral surfaces of the hands and feet are dark brown, and the ventral surfaces of the legs are grayish brown or dull yellowish tan. The belly is dull yellow, heavily suffused with brown or gray; the throat and chest are a dusty cream-color mottled with brown. In females, the dorsum is uniform pale olive-green; the sides of the head and upper surfaces of the limbs are colored like the body. The anterior and posterior surfaces of the thighs are brown with pale yellow spots; the flanks are dark brown with creamy yellow spots. The ventral surfaces of the hind limbs are dull yellow. The ventral surfaces of the forelimbs are dusty yellow, and ventral surfaces of the hands and feet are dull yellow with a suffusion of brown. The belly is bright yellow, and the throat is creamy yellow. In some individuals a narrow, faint white line is present on the upper lip. The iris in both sexes varies from a greenish bronze to a golden bronze or dull copper color.

Some individuals when found by day were pale yellowish tan above; later these changed to green with dark mottling. Most of the specimens that have been examined in life came from Volcán Poás or Volcán Barba. Few differences were noted in the coloration between samples from these two localities. Perhaps the most noticeable difference is that in males from Volcán Barba the belly seems to be more heavily suffused with dark pigment than in those specimens from Volcán Poás. Furthermore, the greenish bronze color of the iris has been noted only in specimens from Volcán Barba.

In preservative the dorsal coloration of males is dull brown with darker brown markings; in females the dorsum is uniform tan or dull brown. In specimens of both sexes, the anterior and posterior surfaces of the thighs and the flanks are dark brown with creamy tan spots. The venter is dull yellowish tan in both sexes, suffused with brown or gray in males. In some females distinct brown spots are present; these were not noticed in living individuals.

TADPOLES: The sizes and proportions of tadpoles of *Hyla pictipes* in relation to the developmental stages are given in table 33. A typical tadpole in developmental stage 38 has a body length of 15.5 mm. and a total length of 42.4 mm. The body is depressed; it is half again as wide as deep. The top of the head is flat and inclined anteriorly from a point above the eyes. The posterior part of the venter is rounded, whereas the anterior part is flat. In dorsal profile the body is bluntly rounded anteriorly and posteriorly; in lateral profile the snout slopes gradually and is acutely rounded. The eyes are small; they are situated dorsally and directed dorsolaterally. The nostrils are about one-fourth the distance from the eyes to the tip of the snout. The spiracle is sinistral and situated about midway

between the eye and the posteroventral edge of the body. The anal tube is short and median. The caudal musculature is robust and extends nearly to the tip of the tail. At mid-length of the tail the depth of the musculature is greater than that of either fin. The dorsal fin does not extend onto the body, and the caudal fin is bluntly rounded terminally (fig. 135).

The mouth is exceedingly large and ventral in position; the lateral edges of the lips are visible from above. A deep lateral fold is present. A single row of small papillae completely borders the mouth. Lying medial to these are two rows of small papillae on the anterior lip and four to six rows on the posterior lip; there are no papillae in the lateral folds. The beaks are rather weak and bear minute serrations. The upper beak is strongly bow-shaped, whereas the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth; all are complete. The upper rows are about equal in length; the lower rows are only slightly, if at all, shorter than the upper rows. The teeth are small and are situated on low, fleshy ridges (fig. 136).

The body is black with golden lichenous markings. The tail musculature is tan and the fins are clear. The iris is black with gold flecks. In preservative, the body is dark brown, slightly paler anteriorly. The caudal musculature is brown, and the caudal fins are transparent with faint brown flecks.

The tadpoles all have two upper and three lower rows of teeth. The rows are approximately equal in length in tadpoles in developmental stage 31 and later stages. In tadpoles in developmental stages 27 and 29, the second upper and first lower rows are noticeably shorter than the others. In one tadpole in developmental stage 25, the two upper and the first lower rows are short.

MATING CALL: The call of *Hyla pictipes*

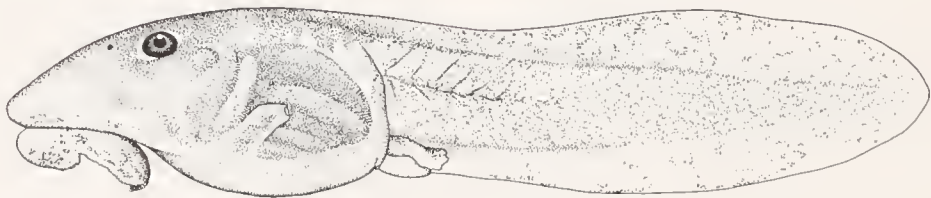


FIG. 135. Tadpole of *Hyla pictipes*, K.U. No. 68437. $\times 3$.

TABLE 33
 Sizes and Proportions, with Means in Parentheses, of Tadpoles of *Hyla pictipes*.

Developmental Stage	N	Body Length	Tail Length	Total Length	Body/Tail
25	1	9.8	16.7	26.5	58.6
27	5	11.0-11.5 (11.2)	17.6-19.5 (18.9)	28.6-30.0 (29.4)	57.6-61.3 (59.1)
29	3	11.5-12.2 (11.8)	20.0-25.0 (22.4)	31.5-37.2 (34.2)	51.3-53.1 (52.6)
31	8	13.0-14.5 (13.9)	22.4-25.5 (24.0)	36.5-40.0 (38.0)	56.8-63.2 (63.1)
35	2	15.1-15.3 (15.2)	26.9-27.4 (27.2)	42.0-42.5 (42.3)	55.8-56.1 (56.0)
38	2	15.5-16.0 (15.8)	26.9-29.0 (28.0)	42.4-45.0 (42.7)	55.2-57.6 (56.4)
40	2	17.0-17.6 (17.3)	27.0-28.6 (27.8)	44.0-46.2 (45.1)	61.5-62.9 (62.2)
43	6	15.6-18.0 (16.8)	7.3-13.8 (9.2)	23.8-30.0 (26.5)	10.1-29.3 (17.2)

consists of a single, pulsed, low-pitched note, which is repeated at intervals of 20 seconds to several minutes. The duration of the note is 0.28 to 0.38 (mean, seven calls, 0.32) of a second. The pulse rate is 110 to 143 (mean, 123) pulses per second, and the dominant frequency varies from 2230 to 2750 (mean, 2591) cycles per second (pl. 23, fig. 1).

NATURAL HISTORY: *Hyla pictipes* inhabits high montane forests that receive abundant moisture throughout the year; the frogs are active year round and possibly breed throughout the year. However, calling males seem to be most abundant in March through May.

The frogs are always found in close proximity to mountain streams. Males call from rocks in and along edges of streams and from the branches of low (usually no more than 1 meter above ground) vegetation. By day, the frogs take refuge beneath rocks at the edges of the streams. Mating activity is carried on at relatively low temperatures; males were calling when the air temperature was between 8 and 18 degrees centigrade.

The tadpoles develop in cold mountain streams, where they cling to the tops or sides of large stones in the streams. When the tadpoles are disturbed, they swim against the strong current and adhere to another rock or take refuge beneath rocks at the bottom of the stream. At the Río Poasito on Volcán Poás, Alajuela Province, Costa Rica, tadpoles of *Hyla pictipes* were found in the same stream with those of *Hyla rivularis*. The tadpoles of these two species are similarly adapted for a stream existence. No different ecological preferences of the tadpoles were observed.

Two recently metamorphosed young were collected on April 17, 1961, at the Río Poasito. These small individuals were found on low vegetation at the edge of a rocky stream at night. The frogs have snout-vent lengths of 20.1 and 20.8 mm. In life, the dorsum was pale greenish brown and the belly and feet were pale yellow. The flanks were brown and

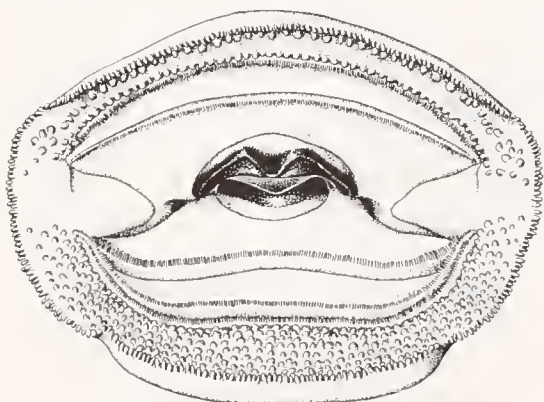


FIG. 136. Mouth of tadpole of *Hyla pictipes*, K.U. No. 68437. $\times 8$.

white; the posterior surfaces of the thighs were yellowish brown with pale yellow spots. Three tadpoles collected at the Río Poasito on May 7, 1961, were transformed in the laboratory. Upon transformation, the frogs had snout-vent lengths of 16.0, 17.0, and 18.4 mm. In life, the dorsum was dull green with a faint brownish tinge middorsally. The hands, feet, and thighs were dark yellow. The venter was creamy yellow and the flanks were cream with brown spots.

REMARKS: Cope (1876) described and named three varieties of *Hyla punctariola*. Dunn (1940b) showed that *punctariola* is actually a species of *Eleutherodactylus*. Starrett

(1966) and Duellman (1966b) pointed out the rediscovery of *Hyla pictipes* and discussed the taxonomic status of the other two varieties (*moesta* and *monticola*) described by Cope.

ETYMOLOGY: The specific name is derived from the Latin *pictilis* meaning painted and the Latin *pes* meaning foot and alludes to the dark pigmentation on the feet.

DISTRIBUTION: *Hyla pictipes* is known from montane forests at elevations of 1900 and 2500 meters in the Cordillera Central of central Costa Rica and on the Pacific slopes of the Cordillera Talamanca in Costa Rica (fig. 137).

See Appendix 1 for the locality records of the 157 specimens examined.

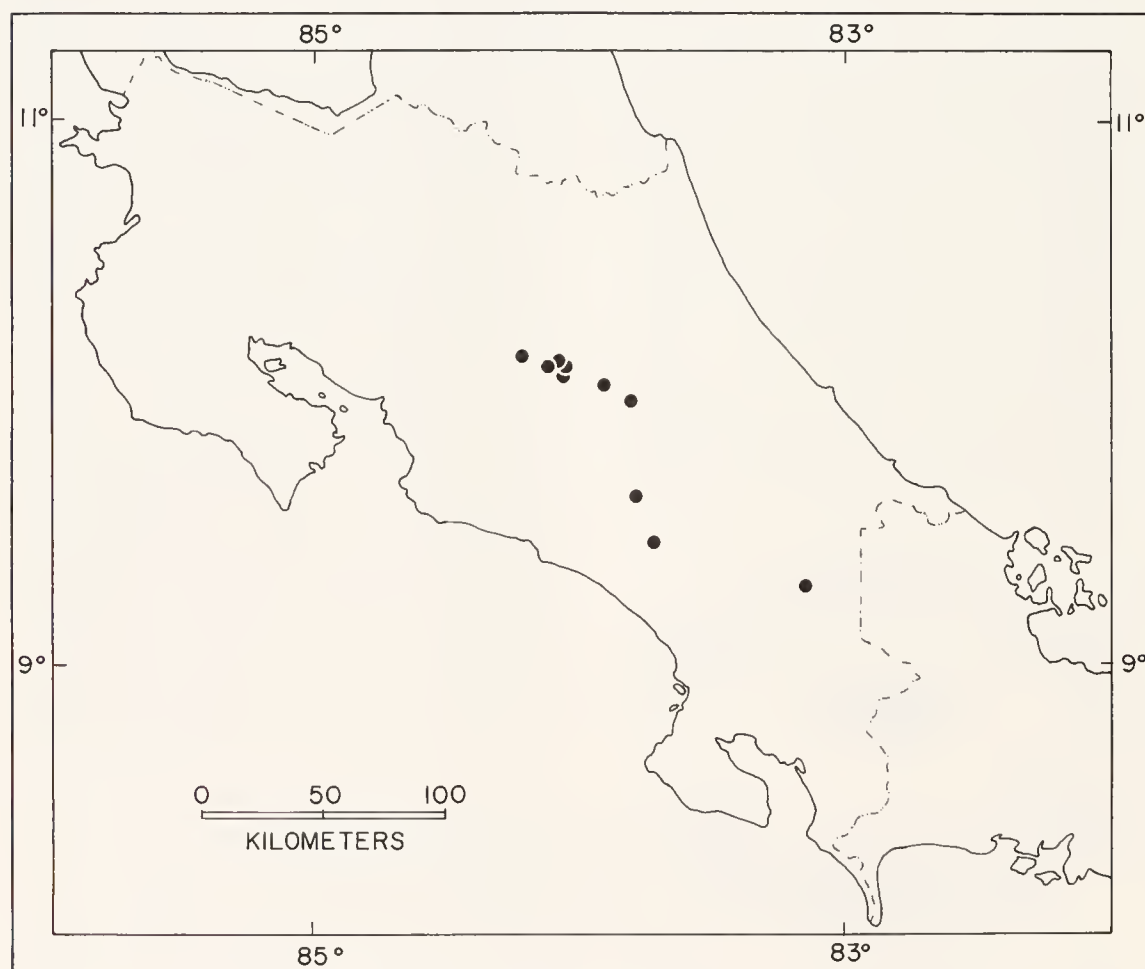


FIG. 137. Distribution of *Hyla pictipes*.

The *Hyla uranochroa* Group

DEFINITION: Members of this group are moderately small stream-breeding species; males attain a maximum snout-vent length of 36.8 mm. and females, 39.9 mm. The dorsum is pale green or olive or reddish brown with a white stripe on the edge of the lip and edges of the forearms and feet. The iris is red, and the palpebral membrane is clear or weakly flecked. The fingers are about one-fourth and the feet, two-thirds webbed. A weak tarsal fold is present, but an axillary membrane and dermal folds or appendages on the limbs are absent. Males have single, median, subgular vocal sacs and horny nuptial excrescences on the prepollices. The skull is only moderately ossified. A large frontoparietal fontanelle is present. The sphenethmoid is broad and short and does not extend anteriorly between the nasals, which are slender, widely separated medially, and not in contact with the sphenethmoid (fig. 138). The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosal extends one-third (*rufioculis*) or one-half (*uranochroa*) of the

distance to the maxillary. The quadratojugal is in contact with the maxillary in *uranochroa* and present only as a spur posteriorly in *rufioculis*. The medial ramus of the pterygoid is in bony contact with the prootic. The prevomers are poorly ossified but bear teeth. The tadpoles have long tails with low fins and large funnel-shaped ventral mouths. The mating call consists of a long series of well-modulated notes or a short rattling series of notes. The haploid number of chromosomes is 12.

COMPOSITION: Two species (*Hyla rufioculis* and *uranochroa*) comprise the group, which is endemic to the highlands of Costa Rica and western Panamá. Of these, 546 preserved frogs, 16 skeletons, and 28 lots of tadpoles have been examined.

COMMENTS: Savage (1968) included in the *uranochroa* group all of those species that I place in the *rivularis*, *pictipes*, and *uranochroa* groups, plus *Hyla legleri*. Because of the presence of a red eye in the adult, *Hyla legleri* formerly has been associated with this group (Starrett, 1966; Savage, 1968). However, *legleri* differs from members of the *Hyla uranochroa* group osteologically and has a distinctly different kind of tadpole; in these characters it closely resembles *salvadorensis* and accordingly is more properly associated with that species.

Both species in the *Hyla uranochroa* group occur on the Caribbean and Pacific slopes of Costa Rica; the two species have different altitudinal ranges. In some areas, *Hyla uranochroa* descends to elevations inhabited by *rufioculis*, so that the two occur sympatrically and even breed in the same streams at the same time. The differences in mating calls probably act to enhance reproductive isolation in sympatric populations. It is likely that the two species differentiated through altitudinal separation rather than one on the Caribbean and the other on the Pacific slopes.

Both the adults and tadpoles of the members of the *Hyla uranochroa* group bear a striking resemblance to *Ptychohyla schmidtorum* in northern Central America. The former differs from *Ptychohyla* by having the nasals separated from, instead of broadly sutured to, the sphenethmoid, by having tadpoles with two, instead of three, upper rows

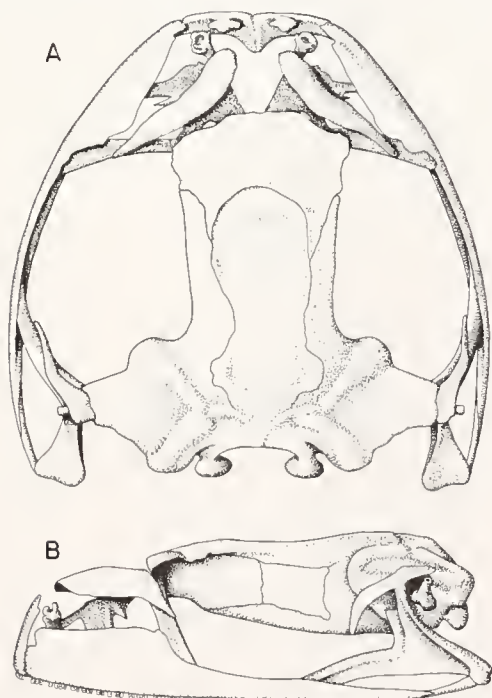


FIG. 138. Dorsal (A) and lateral (B) views of the skull of *Hyla uranochroa*, K.U. No. 117433. $\times 5$.

of teeth, and by lacking ventrolateral glands in breeding males. These similarities seem to be the result of convergence rather than an indication of close relationship.

Hyla uranochroa Cope

Hyla uranochroa Cope, 1876, p. 103 [holotype, U.S.N.M. No. 20651 from near Sipurio, Limón Province, Costa Rica; William M. Gabb collector]. Brocchi, 1882, p. 38. Boulenger, 1882a, p. 377. Günther, 1901 (1885-1902), p. 276. Taylor, 1952c, p. 834. Duellman, 1966, p. 276 [synonymized *Hyla alleci* Taylor with *Hyla uranochroa*].

Hyla alleci Taylor 1952c, p. 831 [holotype, R.C.T. No. 775 from Isla Bonita, Heredia Province, Costa Rica; Richard C. Taylor collector].

DIAGNOSIS: This moderately small green *Hyla* with red eyes, truncate snout, little webbing, and a white lateral stripe is readily distinguished from its apparent closest relative, *rufoculis*, by having a larger tympanum (more than 50 per cent of the diameter of the eye in *uranochroa* and less than 50 per cent in *rufoculis*), longer snout, unpigmented plantar surfaces of the feet, and a straight white labial stripe (expanded below the eye in *rufoculis*). *Hyla legleri* and *erythromma* also have red eyes; the former has more webbing, a dark brown dorsum, and a dark throat in breeding males; the throat in *uranochroa* is yellow in life and white in preservative. *Hyla erythromma* has mottled brown and white flanks, acutely rounded snout, and more webbing than does *uranochroa*.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 36.8 mm., and females reach 39.9 mm. In a series of 21 males from the north slope of Cerro Pando, Bocas del Toro Province, Panamá, the snout-vent length is 31.2 to 36.8 (mean, 34.1) mm.; the ratio of tibia length to snout-vent length is 0.465 to 0.552 (mean, 0.493); the ratio of foot length to snout-vent length is 0.375 to 0.433 (mean, 0.409); the ratio of head length to snout-vent length is 0.325 to 0.350 (mean, 0.335); the ratio of head width to snout-vent length is 0.334 to 0.358 (mean, 0.347), and the ratio of the diameter of the tympanum to that of the eye is 0.588 to 0.765 (mean, 0.661). In 12 females from the same locality, the snout-vent length is 36.3 to 39.9 (mean, 37.8) mm. Females differ from males by having a slightly

larger tympanum; the ratio of the diameter of the tympanum to that of the eye in females is 0.628 to 0.780 (mean, 0.696). Little geographic variation is noticeable in size and proportions. Specimens from the Pacific slopes of the Costa Rican highlands have a slightly shorter hind leg and narrower head, but larger tympanum. In eight males from the south slope of Cerro de la Muerte, Costa Rica, the ratio of tibia length to snout-vent length is 0.446 to 0.484 (mean, 0.468); the ratio of head width to snout-vent length is 0.316 to 0.339 (mean, 0.325), and the ratio of the diameter of the tympanum to that of the eye is 0.657 to 0.714 (mean, 0.693).

The head is noticeably wider than the body, and the top of the head is barely convex. In dorsal and lateral profiles, the snout is truncate. The snout is long; its length is about equal to the length of the orbit. The nostrils are noticeably protuberant and are situated nearly at the tip of the snout; the internarial area is slightly depressed. The canthus is rounded; the loreal region is barely concave, and the lips are moderately thick but not flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper one-fourth of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. A distinct dermal fold is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist. The fingers are moderately short and stout and bear moderate-sized discs; the width of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The subarticular tubercles are large and conical; in many individuals, the distal tubercle on the fourth finger is bifid, and in some specimens, the distal tubercles on the second and third fingers are bifid. The supernumerary tubercles are low and indistinct in many specimens, whereas in others they form multiple rows on the basal segments of each digit. A low bifid palmar tubercle usually is evident. The prepollex is barely enlarged and in breeding males bears

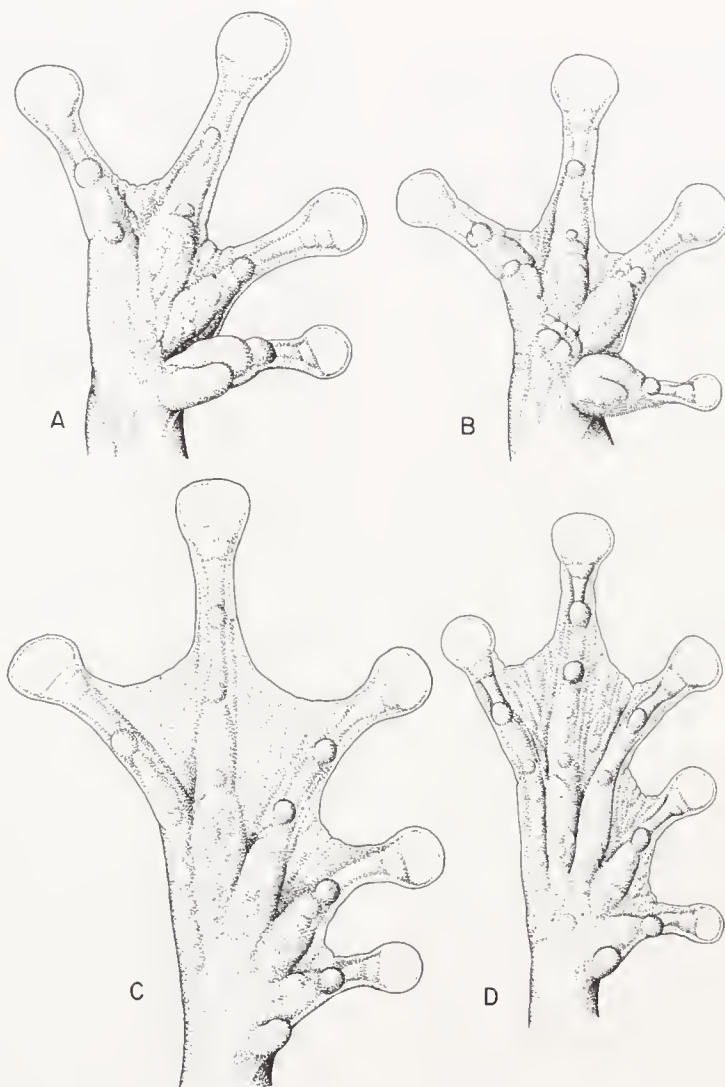


FIG. 139. Hands and feet of members of the *Hyla uranochroa* group. A and C. *Hyla uranochroa*, K.U. No. 103767. B and D. *Hyla rufoculis*, K.U. No. 86453. $\times 5$.

a small, poorly developed nuptial excrescence. The fingers are about one-third webbed (fig. 139A). The webbing is vestigial between the first and second fingers and extends from the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third and on to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends

to the anterior corner of the eye. A transverse dermal fold is present on the heel, and a weak tarsal fold usually is evident distally on the tarsus. The inner metatarsal tubercle is rounded, ovoid, and barely visible from above. The outer metatarsal tubercle, if present, is low and subconical. The toes are moderately long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are moderately large and subconical, and the supernumerary tubercles are small and present only on the proximal seg-

ments of the digits. The toes are about two-thirds webbed (fig. 139C). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs. A short, broad anal sheath above and many large tubercles below the anus are present. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is elongately ovoid, usually emarginate, and not free behind. The dentigerous processes of the prevomers are narrowly separated, posteromedially inclined ridges between the moderately large, ovoid choanae. Males have three to six (mean, 4.8) and females have four to seven (mean, 5.1) teeth on each process. The vocal slits extend from the posterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Hyla uranochroa* is bright green above and yellow below (pl. 54, fig. 3). Usually the dorsum is bright green with or without small yellowish flecks. The ventral surfaces and the anterior and posterior surfaces of the thighs, the inner edges of the feet, the fingers, and first four toes, as well as the webbing, are deep yellow. A narrow white stripe on the upper lip continues to the groin. There is a creamy white stripe on the upper arm and a white stripe on the outer edge of the forearm, the outer edge of the shank, and the outer edge of the foot. A white anal stripe usually is present, and the tubercles below the anal opening are white. The iris is bright red; in some individuals, the palpebral membrane is finely flecked with pale green.

Little variation in coloration is present. Some individuals lack a white anal stripe, and in some specimens, the white labial stripe is expanded below the eye. The intensity of ventral pigment varies in living individuals. In

some specimens, the lower flanks are deep yellow, whereas the midventral region and the throat are pale yellowish white; in all living individuals there is at least a tint of yellow on the venter.

In preservative, the dorsum is dull bluish purple; this color is present on the dorsal surfaces of the arms and basal segments of the fourth finger, as a narrow dorsal stripe on the length of the thigh, on the dorsal surfaces of the shank, feet, and fourth and fifth toes. The anterior and posterior surfaces of the thighs are creamy tan, and the venter is creamy white.

TADPOLES: Several developmental series of tadpoles are available; the growth of the tadpoles in relation to developmental stages is summarized in table 34.

A typical tadpole in developmental stage 26 has a body length of 11.3 mm. and a total length of 33.0 mm. The body is ovoid, slightly depressed, and barely wider than deep. In dorsal profile, the snout is rounded; in lateral profile, the snout is acuminate. The eyes are moderately small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point slightly closer to the eyes than to the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point below the midline about two-thirds of the length of the body. The anal tube is moderately long and dextral. The caudal musculature is robust and extends nearly to the tip of the rounded tail. The caudal fins are low; the dorsal fin does not extend onto the body. At midlength of the tail, the depth of the caudal musculature is noticeably greater than the depth of either fin (fig. 140A).

The body is dull olive-brown with bluish green flecks on the dorsum and flanks. The caudal musculature is pale creamy tan with brown spots. Minute white flecks are present on the tail. The iris is bright red. In preservative, the body is dark brown; the caudal musculature is pale tan with brown flecks. The caudal fins are transparent with small brown flecks, especially dorsally.

The mouth is ventral, large, and funnel-shaped. Lateral folds are lacking, and the mouth is entirely bordered by a row of minute papillae. Large conical papillae are present in the mouth. The beaks are relatively small

TABLE 34
Measurements of Tadpoles, with Means in Parentheses,
in Relation to Developmental Stages, of *Hyla uranochroa*
from Cinchona and Isla Bonita, Costa Rica.

Stage	N	Body Length	Tail Length	Total Length
25	13	5.9-11.0 (8.9)	11.3-26.1 (18.8)	17.2-37.0 (27.6)
26	3	11.2-11.4 (11.3)	20.6-26.8 (23.8)	32.0-38.2 (35.1)
27	2	11.7-11.8 (11.8)	24.2-26.7 (25.5)	36.0-38.4 (37.2)
28	6	11.2-12.8 (12.0)	24.9-27.6 (26.3)	37.1-39.6 (38.3)
29	9	11.6-13.2 (12.2)	26.4-30.0 (27.9)	38.1-43.2 (40.2)
30	9	11.6-13.2 (12.5)	23.2-32.9 (28.8)	35.2-46.0 (41.3)
31	7	12.0-14.7 (13.3)	28.0-36.0 (30.9)	40.7-50.7 (44.2)
32	3	13.0-14.1 (13.4)	29.9-34.8 (32.0)	43.1-48.9 (45.5)
33	2	12.1-13.4 (12.8)	26.8-32.0 (29.4)	38.9-45.4 (42.2)
34	7	13.0-13.8 (13.3)	26.7-32.0 (29.5)	39.8-45.3 (42.8)
35	4	12.4-14.6 (13.5)	25.9-33.3 (30.5)	38.3-50.0 (44.0)
36	3	12.8-13.7 (13.3)	31.8-33.9 (32.6)	44.9-47.6 (45.9)
37	6	12.3-13.7 (13.1)	27.6-32.3 (29.5)	41.2-45.1 (42.6)
38	1	13.6	37.0	50.6
39	2	14.6	32.7-37.7 (35.2)	47.3-52.3 (49.8)
40	7	12.7-14.6 (13.5)	27.5-35.5 (31.6)	40.0-52.3 (47.1)
41	10	13.0-14.7 (14.0)	32.1-39.1 (35.1)	46.4-53.6 (49.1)
42	1	14.9	20.8	35.7
45	1	15.1	3.1	18.2
46	4	17.0-19.8 (18.5)	-----	-----

and bear elongate pointed serrations. The upper beak is in the form of a broad arch lacking lateral processes and having a median ventral notch. The lower beak is slender and broadly V-shaped. There are two upper and two or three lower rows of teeth. The rows are short; none extends much beyond the lateral edge of the beaks. The first upper row

is narrowly interrupted medially, and in some specimens the first lower row is interrupted. The third lower row, when present, is noticeably shorter than the other rows (fig. 141A).

MATING CALL: The call of *Hyla uranochroa* consists of a series of melodic bell-like notes "boop-boop-boop-boop." Recordings are available from the Pacific slopes of Cerro de

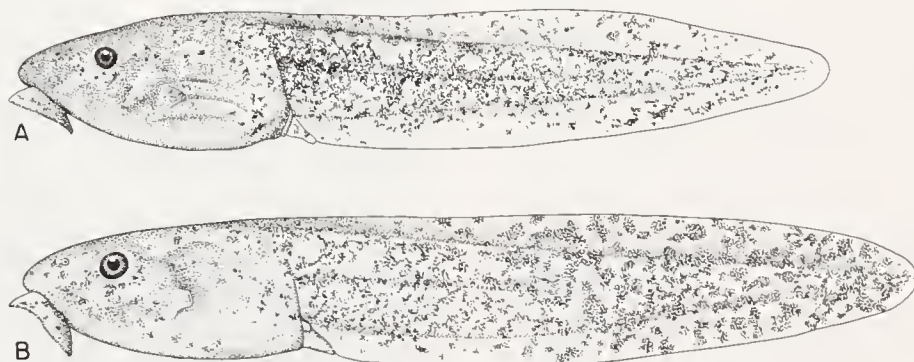


FIG. 140. Tadpoles of members of the *Hyla uranochroa* group. A. *Hyla uranochroa*, K.U. No. 104248. B. *Hyla rufiocularis*, K.U. No. 104159. $\times 3$.

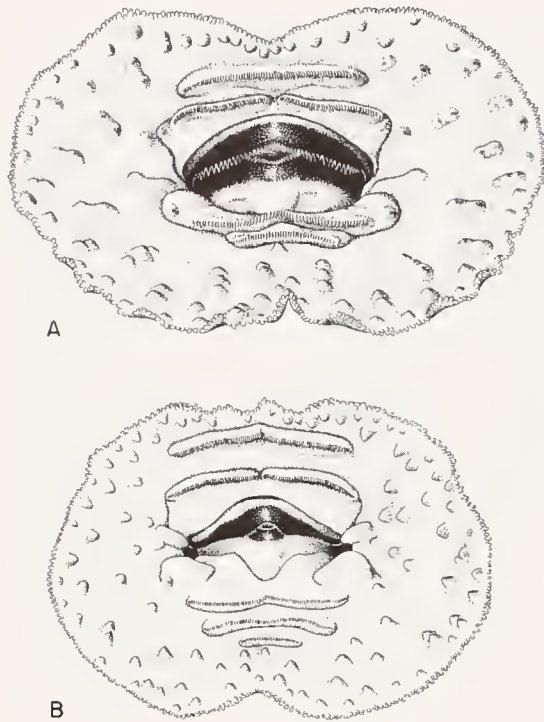


FIG. 141. Mouths of tadpoles of the *Hyla uranochroa* group. A. *Hyla uranochroa*, K.U. No. 104248. B. *Hyla rufoculis*, K.U. No. 104159. $\times 11$.

la Muerte and Cinchona, Costa Rica, and from the north slope of Cerro Pando, Panamá. In recordings from the latter locality, the note repetition rate is 50 and 60 notes per minute, and the notes have a duration of 0.05 and 0.06 of a second. The pulse rate is 240 and 280 pulses per second; the fundamental frequency is 1043 and 1143 cycles per second and the dominant frequency is 2086 and 2226 cycles per second (pl. 21, fig. 3). In the calls from Costa Rica, the note repetition rate is 217 and 264 notes per minute and the duration of the notes is 0.03 and 0.04 of a second. The pulse rate is 240 and 280 pulses per second; the fundamental frequency is 870 and 913 cycles per second, and the dominant frequency is 1740 and 1826 cycles per second (pl. 21, fig. 3).

All these recordings were made at temperatures between 18 and 20 degrees centigrade. Possibly there is geographic variation in the call, or perhaps there are individuals that pro-

duce fast calls and others that produce slow calls.

NATURAL HISTORY: *Hyla uranochroa* is an inhabitant of humid montane forests; the frogs usually are found in the proximity of montane streams. By day, individuals have been found in bromeliads. At night, they congregate along the streams. Calling males usually are in dense vegetation several meters away from the stream. Males seldom call from vegetation at the edge of, or over, the stream. Although this species apparently is active throughout the year, breeding activity seems to reach a peak in May and June.

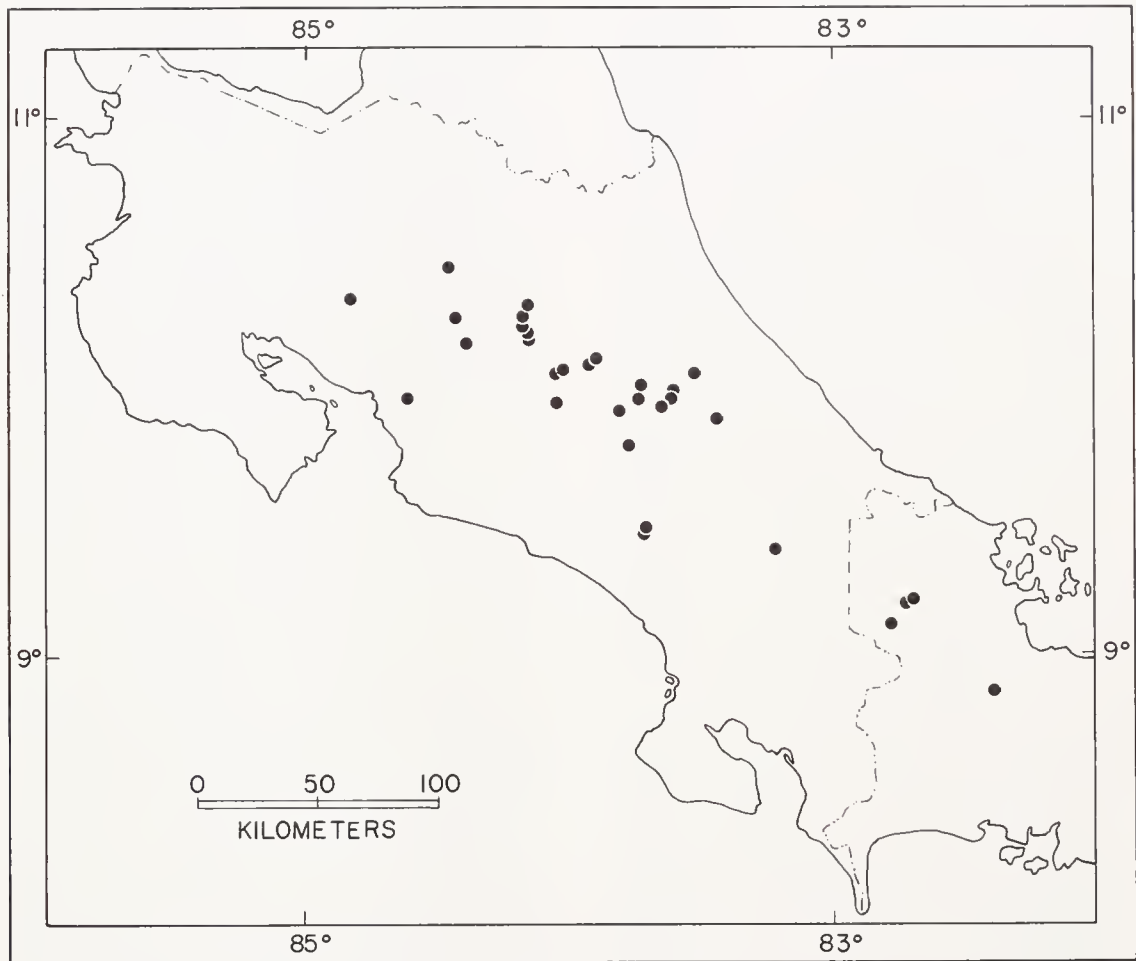
The tadpoles inhabit quiet pools in the stream; they most frequently are found in silt-bottomed pools where they take refuge amidst debris on the bottom.

REMARKS: Taylor (1952c, p. 831) named *Hyla alleei* from Isla Bonita, Heredia Province, Costa Rica. Duellman (1966, p. 276) provided evidence that the characters used by Taylor to diagnose *Hyla alleei* from *uranochroa* are extremely variable and suggested that *Hyla alleei* is a synonym of *Hyla uranochroa*. Savage (1968, p. 15) substantiated this assignment.

ETYMOLOGY: The specific name *uranochroa* is derived from the Greek *ouranos*, meaning sky, and *chroa*, meaning the color of the skin. The name evidently alludes to the blue color of the dorsum in preserved specimens.

DISTRIBUTION: *Hyla uranochroa* inhabits humid montane forests in the mountains of Costa Rica and western Panamá (fig. 142). The total altitudinal range of this species is from 600 to 1720 meters. On the Pacific slopes, which are usually drier than the Caribbean slopes, this species only descends to about 1400 meters, whereas on the Caribbean slopes it descends to 600 meters. At several places throughout the range, *Hyla uranochroa* occurs sympatrically with *Hyla rufoculis*; these places usually are near the upper limits of the range of the latter species. For example, on the southern slopes of Cerro de la Muerte, Costa Rica, *Hyla uranochroa* descends to 1600 meters, the highest elevation attained there by *Hyla rufoculis*.

See Appendix 1 for the locality records of the 202 specimens examined.

FIG. 142. Distribution of *Hyla uranochroa*.***Hyla rufioculis* Taylor**

Hyla rufioculis Taylor, 1952c, p. 827 [holotype, K.U. No. 28216 from Isla Bonita, Heredia Province, Costa Rica; Richard C. Taylor and Edward H. Taylor collectors].

Hyla lythrodus Savage, 1968, p. 1 [holotype, L.A.C.M. No. 26766 from 21 kilometers southwest of Amburi at confluence of the Río Lari and Río Dipnari, Limón Province, Costa Rica; Jay M. Savage and Norman J. Scott, Jr. collectors].

DIAGNOSIS: This moderately small brown or green *Hyla* with red eyes, truncate snout, little webbing, and a white lateral stripe is distinguished from its apparent close relative, *H. uranochroa*, by having a proportionately smaller tympanum (less than 50 per cent of the diameter of the tympanum in *rufioculis* and more than 50 per cent in *uranochroa*),

shorter snout, pigmented plantar surfaces of the feet, and a white labial stripe that usually is expanded below the eye (not expanded in *uranochroa*). *Hyla legleri* and *erythromma* also have red eyes; the former is larger and has more webbing, a darker dorsum, and a dark throat in breeding males; the throat is white in *rufioculis*. *Hyla erythromma* has mottled brown and white flanks, acutely rounded snout, and more webbing than does *rufioculis*.

DESCRIPTION: Males of this small species reach a maximum snout-vent length of 30.0 mm., and females attain 39.9 mm. In a series of 25 males from Finca Moravia, Cartago Province, Costa Rica, the snout-vent length is 25.4 to 28.8 (mean, 26.7) mm.; the ratio of tibia length to snout-vent length is 0.500 to 0.591 (mean, 0.536); the ratio of foot length

to snout-vent length is 0.395 to 0.472 (mean, 0.430); the ratio of head length to snout-vent length is 0.377 to 0.389 (mean, 0.362); the ratio of head width to snout-vent length is 0.354 to 0.394 (mean, 0.372), and the ratio of the diameter of the tympanum to that of the eye is 0.312 to 0.441 (mean, 0.361). In six females from the same locality the snout-vent length is 33.5 to 34.9 (mean, 34.1) mm.; the females do not differ significantly in proportions from the males. Samples were measured from the south slopes of Cerro de la Muerte and from a locality 16 kilometers west-southwest of San Isidro El General, Costa Rica. Males in the former sample were significant in having relatively shorter hind limbs. The ratio of tibia length to snout-vent length is 0.474 to 0.537 (mean, 0.506). In the latter sample, the males are noted for having a smaller tympanum, the ratio of the diameter of the tympanum to that of the eye is 0.302 to 0.356 (mean, 0.332). Two males and three females from El Tigre, Limón Province, Costa Rica are distinctive in their large size. The males have snout-vent lengths of 29.4 and 30.0 mm., and the females have snout-vent lengths of 38.5, 39.2, and 39.9 mm. These frogs differ from other samples by having a relatively larger tympanum; in the five specimens the ratio of the diameter of the tympanum to that of the eye is 0.415 to 0.452 (mean, 0.425). Another individual (L.A.C.M. No. 26766) from the Río Lari, Limón Province, Costa Rica, has a snout-vent length of 30.2 mm. and the ratio of the diameter of the tympanum to that of the eye, 0.555.

The head is slightly wider than the body, the top of the head is barely convex. The snout is truncate in dorsal and lateral profiles. The snout is moderately long; its length is equal to about three-fourths of that of the orbit. The nostrils are slightly protuberant at a point near the tip of the snout; the internarial area is noticeably depressed. The canthus is round; the loreal region is barely concave, and the lips are moderately thick and not noticeably flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a

distance equal to half again the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. In some individuals, small tubercles tend to form an indistinct row along the ventrolateral edge of the forearm; a thin transverse dermal fold is evident on the wrist in some individuals. The fingers are moderately long and slender and bear small discs; the width of the disc on the third finger is equal to the diameter of the eye. The subarticular tubercles are small and subconical; the distal tubercle on the fourth finger is bifid in most individuals, and in some specimens, the distal tubercle on the third finger is weakly bifid. The supernumerary tubercles are small, indistinct, and numerous on the proximal segments of each digit. A moderately elevated, usually bifid, palmar tubercle is present. The prepollex is barely enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about one-fourth webbed (fig. 139B). The webbing is vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third and on to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to a point just anterior to the eye. A thin, transverse dermal fold is present on the heel, and a weak tarsal fold is present distally on the tarsus; in some specimens, there is no evidence of a tarsal fold. The inner metatarsal tubercle is rounded, ovoid, and barely visible from above. Usually a distinct outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately small and subconical, and the supernumerary tubercles are low and indistinct. The toes are about two-thirds webbed (fig. 139D). The webbing extends from the base of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third,

from the middle of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs. A short, broad anal sheath is present, and numerous small tubercles are present below the anal opening. The skin on the throat, belly, and posteroventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is elongately ovoid or narrowly cordiform, shallowly notched posteriorly and barely free behind. The denticulous processes of the prevomers are widely separated, postero-medially inclined ridges between the large ovoid choanae. Males have two to five (mean, 3.0) and females, four to six (mean, 4.9) teeth on each process. The vocal slits extend from the posterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and only moderately distensible.

The general coloration of *Hyla rufoculis* is dull brown or olive-green above and creamy white below (pl. 54, fig. 1). Most individuals are olive-green or dull brown above, but some specimens are bright green above. A silvery white line is present on the margin of the upper lips and extends to the groin. In most specimens, this stripe is expanded below the eye. A narrow white stripe is present on the outer edge of the forearm and outer edge of the tarsus. The elbows, heels, and knees are white and an elongate white mark is present on the dorsal surface of the upper arm. The anterior and posterior surfaces of the thighs are dull tan. A pair of white spots are present above the anal opening in most specimens, whereas in some others, there are no marks whatsoever. The belly is creamy white, and the vocal sac is white. The iris is bright red.

In preservative, the dorsum varies from dull reddish brown to dull bluish purple. This color diminishes on the dorsal surfaces of the thighs, and in approximately half of the specimens, invades the posterior surfaces of the thighs. The ventral surfaces are pale creamy white, and the stripes on the lips, limbs, and flanks are white. In most specimens, there is some dark demarcation between the creamy white venter and the white lateral stripe. This

usually is most evident in the axillary region and consists of a narrow brown line or series of dashes.

TADPOLES: A developmental series of tadpoles is available from a stream 15 kilometers west-southwest of San Isidro el General, Costa Rica (table 35).

A typical tadpole in developmental stage 28 has a body length of 11.4 mm. and a total length of 38.3 mm. The body is broadly ovoid and slightly wider than deep. In dorsal profile the snout is bluntly round, and in lateral profile it is acutely round. The eyes are moderately small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point just below the midline and just posterior to the midlength of the body. The caudal musculature and fins extend nearly to the tip of the rounded tail. The fins are shallow, and the dorsal fin does not extend on to the body. At midlength of the tail, the depth of the caudal musculature is equal to the combined depth of the dorsal and ventral fins (fig. 140B).

The dorsum is dull olive-brown, and the flanks are somewhat paler with bluish white flecks. The caudal musculature is pale brown with a heavy suffusion of brown flecks and small spots, which also extends onto the fins. The iris is red. In preservative, the body is brown, and the caudal musculature is pale tan with dark brown flecks.

The mouth is ventral, large, and funnel-shaped. The lips are completely bordered by a single row of minute papillae; lateral folds are lacking. Numerous large papillae are present in the mouth. The beaks are moderately robust and bear long, pointed serrations. The upper beak is in the form of a broad arch without lateral processes, and the lower beak is broadly V-shaped. There are two upper and two or three lower rows of teeth. The rows are short and barely extend beyond the lateral extent of the beaks. The first upper tooth row is narrowly interrupted medially. The second row and, when present, third lower tooth row are shorter than the first lower row (fig. 141B).

MATING CALL: The call of *Hyla rufoculis*

TABLE 35
Measurements of Tadpoles, with Means in Parentheses,
in Relation to Developmental Stages, of *Hyla rufiocularis*
from 15 Kilometers West-Southwest of
San Isidro El General, Costa Rica.

Stage	N	Body Length	Tail Length	Total Length
25	11	4.7-11.6 (8.3)	9.6-26.5 (18.1)	14.3-38.1 (23.7)
26	3	9.1-11.6 (10.1)	18.5-25.6 (21.7)	27.6-37.2 (31.8)
27	3	10.1-10.8 (10.5)	20.5-22.9 (22.0)	31.2-33.7 (32.5)
28	3	10.1-11.8 (11.1)	23.6-27.0 (23.8)	33.7-38.3 (35.9)
29	2	12.0-12.4 (12.2)	25.6-28.9 (27.3)	37.6-41.3 (39.5)
31	2	11.6-11.8 (11.7)	26.8-27.7 (27.3)	38.6-39.3 (39.0)
32	1	12.0	25.6	37.6
34	1	11.9	27.7	39.6
35	4	12.4-13.0 (12.8)	19.0-30.5 (26.2)	31.8-43.5 (39.0)
37	2	12.0-13.0 (12.5)	26.8-30.0 (29.4)	38.8-43.0 (40.9)
40	2	12.8	30.8-31.7 (31.3)	43.6-44.5 (44.1)
41	3	11.6-11.8 (11.7)	22.6-31.2 (27.3)	34.3-43.0 (38.9)
44	1	14.7	18.7	33.4
46	3	15.5-16.1 (15.9)	-----	-----

consists of a short rattle. Each call group consists of three or four short notes. The interval between call groups varies from three to 18 (mean, 6.1) seconds. The duration of notes is 0.05 to 0.07 (mean, 0.06) of a second. The fundamental frequency varies from 78 to 95 (mean, 87) cycles per second, and the dominant frequency varies from 2070 to 2570 (mean, 2320) cycles per second (pl. 22, fig. 1).

NATURAL HISTORY: *Hyla rufiocularis* is an inhabitant of humid montane forests where this species is active throughout the year, except at times of little rain. Males call from branches of bushes at the edge of, or over, small streams.

The tadpoles develop in quiet pools in the stream, where they seek refuge amidst debris on the bottom of the pools.

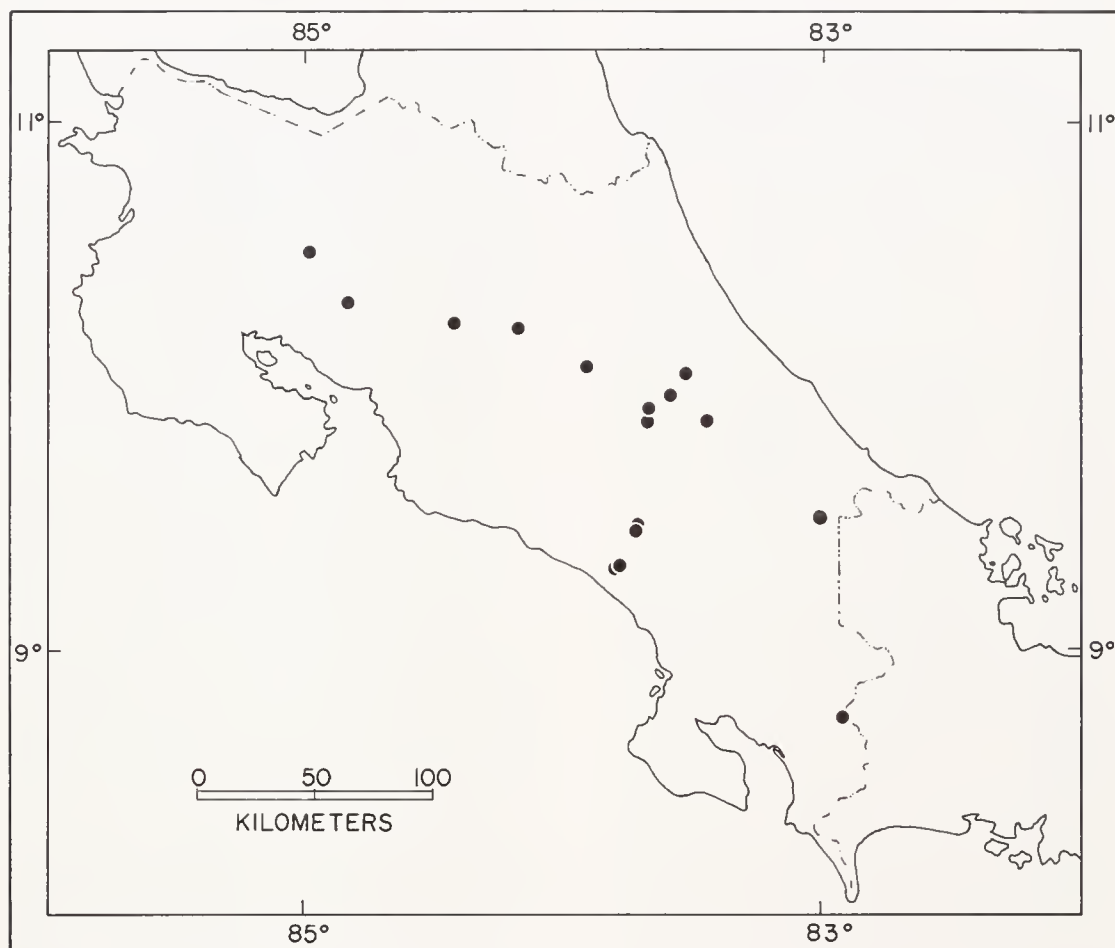
REMARKS: Savage (1968, p. 1) named *Hyla lythrodes* on the basis of a single male from the Río Lari, Limón Province, Costa Rica. Savage stated that *lythrodes* "approaches *rufiocularis* of Atlantic and Pacific Costa Rica but is distinct in morphology and limb coloration. *H. rufiocularis* has a small tympanum, scarcely larger than the largest finger disc and less than one-third the diameter of the orbit and the posterior surface of the thighs suffused with dark pigment."

Examination of the holotype of *Hyla lythrodes* (L.A.C.M. No. 26766) reveals only

one character that will separate this specimen from the several large series of *H. rufiocularis* that have been examined. The holotype of *lythrodes* has a relatively large tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.555. The highest ratio in any specimen assigned to *rufiocularis* is 0.441. The coloration on the posterior surface of the thighs (light in *lythrodes* and supposedly dark in *rufiocularis*) is highly variable in *rufiocularis*. Except for the proportionately large tympanum, I can find no characters by which to separate *lythrodes* from *rufiocularis* and suggest that *lythrodes* be placed in the synonymy of *Hyla rufiocularis*. This assignment might be proven to be incorrect on the basis of presently unavailable biological information. Savage (1968, p. 6) stated that the call of the single male of *lythrodes* differed from the calls of *rufiocularis* and *uranochroa*. The absence of recordings precludes an objective comparison.

ETYMOLOGY: The specific name is derived from the Latin *rufus*, meaning red, and the Latin *oculus*, meaning eye, and refers to the red eye that is characteristic of this species.

DISTRIBUTION: *Hyla rufiocularis* inhabits the Atlantic and Pacific slopes of all of the mountain ranges in Costa Rica from elevations of 775 meters to 1580 meters (fig. 143).

FIG. 143. Distribution of *Hyla rufoculis*.

See Appendix 1 for the locality records of the 388 specimens examined.

The *Hyla lancasteri* Group

DEFINITION: The frogs comprising this group are moderately small stream-breeders; males attain a snout-vent length of 33.6 mm. and females, 41.1 mm. The dorsum is mottled shades of brown or green and gray. The dorsal surfaces of the limbs are marked by transverse bars, and the anterior and posterior surfaces of the thighs are white or yellow with black spots or vertical bars. The venter is white and heavily mottled with black in some populations. The palpebral membrane is clear. The snout is exceedingly short and truncate. The fingers are about one-third webbed, and

the toes are about three-fourths webbed. A well-developed tarsal fold is present, but an axillary membrane is absent. Dermal fleshy protuberances are present on the dorsum and on the limbs in some populations. Males have a single, median, subgular vocal sac and horny nuptial excrescences on the prepollices. The skull is moderately well ossified with a small ovoid frontoparietal fontanelle (fig. 144). The sphenethmoid is large and broad and does not extend anteriorly between the small, slender nasals, which articulate with the sphenethmoid anterolaterally. A quadratojugal is present. The squamosal articulates with the crista parotica, and the anterior arm of the squamosal extends about one-third of the distance to the maxillary. The medial ramus of the pterygoid is in bony contact with the prootic. The pre-

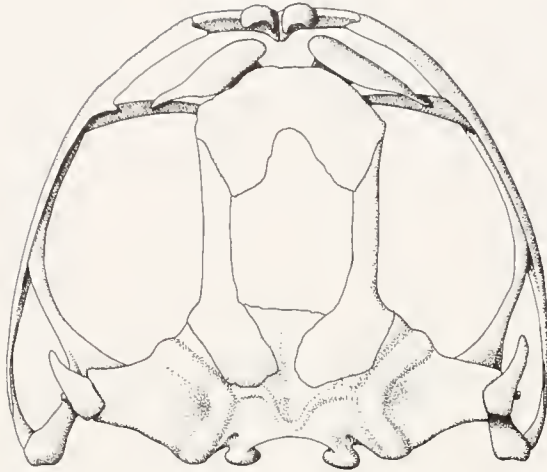


FIG. 144. Dorsal view of the skull of *Hyla lancasteri*, K.U. No. 101601. $\times 6$.

vomers articulate anteriorly and bear large, transverse dentigerous processes. The tadpoles have moderately long muscular tails and moderately enlarged ventral mouths with two upper and three lower rows of teeth. The mating call consists of a single or paired rattling note. The number of chromosomes is unknown.

COMPOSITION: One species, *Hyla lancasteri*, is included in this group, which is endemic to the Caribbean slopes of Costa Rica and western Panamá. One hundred ninety-five preserved frogs, eight skeletons, 15 lots of tadpoles, and three preserved clutches of eggs have been examined.

COMMENTS: *Hyla lancasteri* is another of the Middle American species that apparently has no close relatives. Superficially, *lancasteri* is similar to the Mexican *Hyla thorectes*; furthermore, both species deposit eggs on vegetation above streams and have relatively unspecialized stream tadpoles. *Hyla thorectes* has more reduced cranial elements than *lancasteri*; in the former the quadratojugal is absent, the squamosal is not in bony contact with the crista parotica, and the medial ramus of the pterygoid does not have a bony articulation with the prootic.

Bokermann (1964) suggested that *Hyla moraviaensis* (= *lancasteri*) is related to the Amazonian *Hyla marmorata*. The latter has a short, truncate snout like that of *lancasteri*, but *marmorata* has extensive webbing, axillary membranes and fringes on the limbs; the tad-

poles are pelagic types with a terminal mouth and deep fins on the xiphicercal tail.

Hyla lancasteri Barbour

Hyla lancasteri Barbour, 1928, p. 31 [holotype, M.C.Z. 13062 from Peralta, Cartago Province, Costa Rica; C. R. Lancaster collector]. Duellman, 1966b, p. 271 [synonymized *Hyla moraviaensis* Taylor, 1952, with *Hyla lancasteri* Barbour, 1928]. Trueb, 1968a, p. 285.

Hyla boulengeri (in part): Dunn and Emlen, 1932, p. 25. Taylor, 1952c, p. 856. Cochran and Goin, 1970, p. 243.

Hyla moraviaensis Taylor, 1952c, p. 865 [holotype, K.U. No. 30284 from Moravia, Cartago Province, Costa Rica; Edward H. Taylor collector].

DIAGNOSIS: This moderately small species differs from all other Middle American hylids by having an extremely short, truncate snout. The dorsum is mottled brown or green and gray, and the anterior and posterior surfaces of the thighs are yellow with black vertical bars or white with black spots. *Hyla boulengeri* and *rostrata* have vertical black bars on the thighs, but both of these frogs have long, protruding snouts. *Hyla thorectes* has a short, truncate snout but lacks vertical bars on the thighs.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 33.6 mm. and females reach 41.1 mm. In a series of 23 males from 3 kilometers south of Pavones, Cartago Province, Costa Rica, the snout-vent length is 27.6 to 31.5 (mean, 29.1) mm.; the ratio of tibia length to snout-vent length is 0.490 to 0.557 (mean, 0.517); the ratio of foot length to snout-vent length is 0.311 to 0.434 (mean, 0.413); the ratio of head length to snout-vent length is 0.242 to 0.336 (mean, 0.304); the ratio of head width to snout-vent length is 0.322 to 0.373 (mean, 0.345), and the ratio of the diameter of the tympanum to that of the eye is 0.429 to 0.588 (mean, 0.471). One female from the same locality has a snout-vent length of 37.5 mm. and does not differ significantly from the males in proportions. Throughout the range of the species in the Caribbean foothills of Costa Rica and western Panamá there is little variation in size and proportions; however, in the highlands of western Panamá there are some noticeable differences. For example, on Cerro Pando, in

extreme western Panamá, there is an altitudinal decrease in snout-vent length, head length, diameter of the tympanum, and diameter of the eye, but there is no significant change in head width or in foot length. These differences are illustrated in a series of eight males from an elevation of 1920 meters on the north slopes of Cerro Pando, Bocas del Toro Province, Panamá. The snout-vent length is 28.0 to 30.6 (mean, 28.9) mm.; the ratio of tibia length to snout-vent length is 0.520 to 0.567 (mean, 0.543); the ratio of foot length to snout-vent length is 0.435 to 0.487 (mean, 0.466); the ratio of head length to snout-vent length is 0.304 to 0.330 (mean, 0.318); the ratio of head width to snout-vent length is 0.337 to 0.382 (mean, 0.363), and the ratio of the diameter of the tympanum to that of the eye is 0.371 to 0.429 (mean, 0.397). Trueb (1968a) gave a detailed statistical analysis of the altitudinal variation in measurements of this species.

The head is as wide as the body, and the top of the head is flat. The eyes are large and prominent. In dorsal profile, the snout is truncate; in lateral profile, it is truncate and barely posteroventrally inclined. The snout is extremely short, and the nostrils are noticeably protuberant at the anterior extremity of the snout. The distance between the anterior edge of the eye and the nostril is approximately equal to the diameter of the eye. The canthus is angular, and the loreal region is barely concave; the lips are thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately long and robust; an axillary membrane is absent. A row of small tubercles is present on the ventrolateral edge of the forearm, and a transverse dermal fold is present on the wrist. The fingers are moderately long and robust and bear moderately large discs; the width of the disc on the third finger is slightly larger than the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; the dis-

tal tubercle on the fourth finger is bifid in most specimens. The supernumerary tubercles are large and subconical. In specimens from high elevations on Cerro Pando many granules are present on the palmar surfaces of the hands. A bifid or tripartite palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrescence. In specimens, from the lowlands, this excrescence is composed of minute spinules, whereas in specimens from high elevations on Cerro Pando, the excrescence is made up of a few large spines. The fingers are about one-third webbed in lowland populations (fig. 145A), and about half webbed in specimens from high elevations on Cerro Pando (fig. 145B). In both populations, the webbing between the first and second fingers is vestigial; in lowland populations, the webbing extends from the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third and from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger, whereas in specimens from high elevations on Cerro Pando, the webbing extends from the base of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third and from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fourth to one-third of the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A transverse dermal fold is present on the heel, and a weak tarsal fold is evident on the distal half of the tarsus. The inner metatarsal tubercle is low, flat, and elliptical; the outer metatarsal tubercle is small and subconical. The toes are moderately short and robust and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are moderately large and subconical, and the supernumerary tubercles are nearly as large as the subarticular tubercles and conical in shape. The toes are about three-fourths webbed (fig. 145C and D). The webbing extends from the middle of the penultimate phalanx of the first toe to the distal end of the antepenultimate



FIG. 145. Hands and feet of *Hyla lancasteri* from lowlands (A and C, K.U. No. 103672) and Cerro Pando (B and D, K.U. No. 101736). $\times 6$.

phalanx of the second, from the distal end of the antepenultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs. A short, narrow anal sheath is present. The chest, belly, and proximal posteroventral surfaces of the thighs are strongly granular. In individuals from the lowlands, the skin on the top of the head and on the back is weakly tuberculate; elsewhere, the skin is smooth. In specimens from high elevations on Cerro Pando the dorsal surfaces of the head, body, forearms, shanks, and feet, are covered with large fleshy protuberances that give the impression of spines. Usually three large pointed tubercles are present on the upper eyelid and two or more are present on the top of the head between the eyes. At least two large spines are present in the scapular region, and smaller spines are present elsewhere on the dorsum. A row of spines is present on the dorsolateral edge of the forearm, and a similar row is present on the dorsolateral edge of the shank and outer edge of the foot. The tongue is nearly round or broadly cordiform, shallowly notched posteriorly, and barely free behind. The denticulous processes of the prevomers are short transverse elevations between the posterior margins of the small ovoid choanae. Males have three to five teeth on each process and a total of six to nine (mean, 7.5) prevomerine teeth; females have six or seven teeth on each process and a total of 12 to 14 (mean, 13.0) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla lancasteri* in the Caribbean foothills is mottled green and brown dorsally with black and yellow flash marks on the thighs (pl. 54, fig. 2). When active at night the dorsum in most individuals is dark metallic green with brown flecks. By day, the dorsum varies from pale tan to metallic green with brown spots or mottling. The groin, anterior and posterior surfaces of the

thighs, the inner edges of the shanks and tarsi are bright yellow with black bars. The anal region is white. The chin and chest are silvery white, and the belly and ventral surfaces of the limbs are grayish white. The iris is reddish brown.

The general coloration of individuals from high elevations on Cerro Pando is green with brown flecks dorsally and lacks yellow pigment on the thighs (pl. 54, fig. 4). In most individuals from Cerro Pando, the dorsum is green with brown flecks and blotches. In some individuals, the tip of the snout is olive-green. The lips are barred with metallic greenish white and dark brown. The posterior part of the eyelid, angle of the jaw, tympanum, and the anterior part of the flanks are dark brown. The posterior part of the flank and the groin are white with dark brown spots. The dorsal surfaces of the thighs are greenish white with dark brown bars. The dorsal surfaces of the forelimbs, shanks, and tarsi are pale green with olive-brown bands. The fingers and toes are tan with brown markings. The chin, throat, and chest are white. The edge of the chin is marked with dark brown. The chest is spotted with black. The skin on the belly, ventral surfaces of the limbs, anterior and posterior surfaces of the thighs, and the axilla lacks pigment, except the white flecks and black spots. The iris is pale cream with copper-colored flecks dispersed throughout, but most concentrated in an anterior and posterior triangle with apices at the pupil.

The coloration described for the lowland population is relatively constant throughout the foothills on the Caribbean slopes of Costa Rica and western Panamá. At elevations of 830 meters on the Río Changena, Bocas del Toro Province, Panamá, the lowland coloration holds. The condition described for populations at high elevations on Cerro Pando hold for individuals taken at elevations between 1450 and 1920 meters on the north slope of Cerro Pando. Individuals from the Río Claro at an elevation of 910 meters are intermediate between the two color types described (see Trueb, 1968a, for detailed comparison).

In preservative individuals from the lowlands and highlands alike generally are dull brown above with darker brown spots or mottling. The posterior part of the flanks and

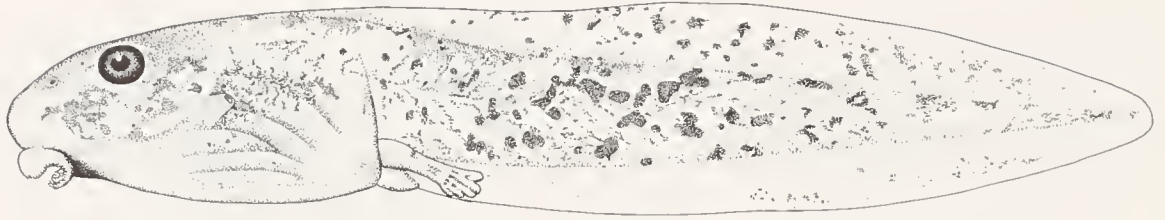


FIG. 146. Tadpole of *Hyla lancasteri*, K.U. No. 104254. $\times 10$.

groin are white with dark brown or black mottling. Distinct transverse bands are evident on the limbs. The venter is creamy white and spotted with dark brown or black in individuals from the highlands.

TADPOLES: The tadpoles of *Hyla lancasteri* are exceedingly large. Tadpoles in developmental stage 25 have total lengths up to 36 mm.; the largest tadpole examined is in developmental stage 41 and has a total length of 55 mm. A typical tadpole in developmental stage 37 has a body length of 16.2 mm. and a total length of 49.8 mm. The body is moderately depressed and only slightly wider than deep. In dorsal profile, the body is ovoid, widest just posterior to the eyes. The snout is bluntly rounded in dorsal profile and acutely rounded in lateral profile. The eyes are moderately large, broadly separated, and directed dorsolaterally. The nostrils are slightly protuberant, directed anterolaterally, and situated about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly on the midline at a point about two-thirds of the distance from the tip of the snout to the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is heavy and terminates somewhat short of the acutely rounded tail. The fins are moderately shallow; at midlength of the tail, the depth of the caudal musculature is somewhat greater than the depth of either fin. The dorsal fin does not extend onto the body (fig. 146).

In tadpoles from a stream 3 kilometers south of Pavones, Cartago Province, Costa Rica, the dorsum is olive-brown with dark brown spots and green lichenous markings. The caudal musculature is tan with dark brown markings. The coloration of tadpoles from a stream at an elevation of 1450 meters on the north slope of Cerro Pando, Bocas

del Toro Province, Panamá, is more intense. The body is olive-brown with dark brown blotches and reticulations. The belly is pale bluish white. The caudal musculature is tan with bold dark brown spots, and the iris is pale bronze. In preservative, the dorsum of the body is brown with a pair of longitudinal creamy tan areas commencing just posterior to the level of the eyes and extending to the posterior edge of the body. Numerous dark brown flecks and blotches are present on the dorsum and sides of the body. The venter is bluish gray with faint white flecks. The caudal musculature is creamy tan with dark brown blotches and flecks. The blotches tend to form transverse bars on the dorsal surfaces of the caudal musculature. Dark brown flecks are present on the dorsal fin and distally on the ventral fin.

The mouth is ventral and rather small; its greatest width is equal to about three-fifths of the greatest width of the body. The lips are completely bordered by two rows of small papillae; lateral folds are present in the lips. Additional papillae are present in the lateral folds. The beaks are small but robust and bear long, conical serrations. The upper beak is in the form of a broad arch with moderately robust lateral processes; the lower beak is massive and U-shaped. There are two upper and three lower rows of teeth. The upper rows are long and extend laterally to the margins of the lips. The second upper row is narrowly interrupted medially. The lower rows are shorter than the upper rows, approximately equal in length, and complete (fig. 147).

The tadpoles of this species were first described by Starrett (1960a, p. 21) under the name of *Hyla moraviensis* (sic.).

MATING CALL: The call of *Hyla lancasteri* at lower elevations in Costa Rica and Panamá

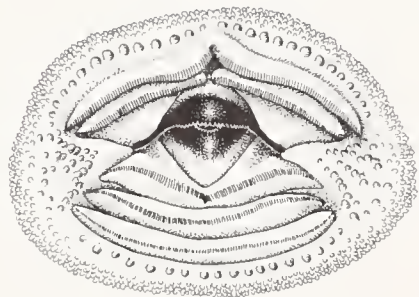


FIG. 147. Mouth of tadpole of *Hyla lancasteri*, K.U. No. 104254. $\times 10$.

consists of a pair of short, high-pitched, poorly modulated notes, characterized by rapid pulsation and usually three emphasized harmonics above the dominant frequency. The call at high elevations on Cerro Pando consists of a single longer note that has a slower pulse rate and only one emphasized harmonic above the dominant frequency (pl. 24, figs. 1 and 2). Seven recordings obtained at Pavones, Costa Rica, at temperatures of 21.7 to 22.2 degrees centigrade have note repetition rates of seven to 19 (mean, 12.5) notes per minute. The duration of the note varies from 0.01 to 0.08 (mean, 0.07) of a second, and the pulse rate varies from 135 to 160 (mean, 150) pulses per second; the dominant frequency varies from 1363 to 1727 (mean, 1525) cycles per second. Two recordings were obtained at an elevation of 1450 meters on Cerro Pando at the temperature of 16.7 degrees centigrade; these had a note repetition rate of 2.6 and 3.6 notes per minute. The notes have durations of 0.35 and 0.37 of a second, and the pulse rate is 90 to 95 pulses per second. The dominant frequency is 1136 and 1181 cycles per second. The differences noted with the increased altitude are characteristic of the differences found with change in temperature.

NATURAL HISTORY: *Hyla lancasteri* inhabits humid montane forests characterized by rainfall throughout the year. Taylor (1952c, p. 868) obtained calling males at Moravia, Cartago Province, Costa Rica, in August, 1951. Starrett (1960a, p. 21) reported calling males from various localities in Cartago Province, Costa Rica, in July and August, 1957. I have found males calling in Cartago Province, Costa Rica, in the months of March through July.

Males were calling at elevations of 1450 and 1920 meters on Cerro Pando in May, 1966.

Tadpoles and recently metamorphosed young were obtained at an elevation of 740 meters in Cartago Province, Costa Rica, in March; Starrett (1960a, p. 21) obtained tadpoles on July 25 at an elevation of 926 meters on the south slope of Volcán Turrialba in Costa Rica. Trueb (1968a) noted that tadpoles and metamorphosing young were abundant in late May at elevations of 830 and 910 meters in western Panamá and that at higher elevations, young tadpoles, eggs, and gravid females were found in early May. She suggested that these data indicate that at lower elevations, breeding starts earlier in the year and possibly is most intense in the months of January and February, whereas at higher elevations, breeding activity seems to be postponed until the start of the rainy season in late April and early May.

At low elevations in Costa Rica and Panamá, males call from low vegetation, the ground, and stones in and along small streams. At high elevations on Cerro Pando, where the limbs of bushes and trees are covered with heavy growths of moss, males typically call amidst the moss on the branches of trees overhanging streams.

Eggs have not been found at low elevations, but at 1450 and 1920 meters on the north slope of Cerro Pando, clutches of eggs were found on leaves up to heights of 2 meters above the streams. Two clutches have 20 and 23 eggs each. Each egg is contained within its own envelope and is slightly more than 6 mm. in diameter. The eggs are deposited in bunches on the upper surfaces of leaves (pl. 8, fig. 2). Trueb (1968a) suggested that the eggs probably are deposited in streams at lower elevations, because no eggs were observed on overhanging vegetation, although breeding activity was underway.

The tadpoles develop in streams. In the rapidly moving streams at higher elevations the tadpoles are particularly found in shallow, gravel-bottomed pools; when disturbed, they take refuge amidst leaves and other debris on the bottom of the pools. The tadpoles living in the slower streams at lower elevations usually were found in quiet, silt-bottomed pools. Large individuals characteristically

concealed themselves beneath stones and debris whereas small tadpoles were found adhering with their mouths to the tops of stones or to leaves in the bottom of the small pool.

REMARKS: Trueb (1968a) discussed in detail the striking character gradients in size, tuberosity, morphological characters of the hands and feet, coloration, mating call, and breeding behavior in this species on Cerro Pando in Panamá; she pointed out that most of the clinal variation seems to be associated with environmental changes of temperature and habitat.

When Trueb and I, accompanied by Charles W. Myers, obtained the first specimen of the "spiny frog" on Cerro Pando in early May, 1966, we all felt that we had obtained a striking new species of tree frog. It was with some dismay, but considerable interest, that we traced the "spiny frog" down the mountain to *Hyla lancasteri*. The altitudinal gradients in morphology, coloration, and behavior in this species are the most striking in any known frog. The changes in tuberosity and coloration are especially well correlated with the density of moss on tree branches at higher elevations.

Barbour (1928, p. 31) named *Hyla lancasteri* on the basis on one juvenile having a snout-vent length of 19.1 mm. Dunn and Emlen (1932, p. 25) placed *lancasteri* in the synonymy of *Hyla boulengeri*. Taylor (1952c, p. 868) questioned the allocation of *Hyla lancasteri* and went on to name *Hyla moraviaensis*. Duellman (1966b, p. 271) noted that the type of *Hyla lancasteri* was not a juvenile specimen of *boulengeri* but instead was a juvenile of the species named *Hyla moraviaensis* by Taylor.

ETYMOLOGY: The specific name is a patronym for C. R. Lancaster, the collector of the type specimen.

DISTRIBUTION: *Hyla lancasteri* occurs at elevations between 650 and 1920 meters on the Caribbean slopes of the highlands of Costa Rica and extreme western Panamá (fig. 148).

See Appendix 1 for the locality records of the 221 specimens examined.

The *Hyla zeteki* Group

DEFINITION: The members of this group are small bromeliad inhabitants; males attain

a maximum snout-vent length of 32.8 mm. and females, 35.2 mm. The dorsum is yellowish or orange-tan or pale brown with no distinctive markings. The palpebral membrane is clear. The webbing is vestigial on the fingers, and the toes are no more than half webbed. Dermal fringes and appendages are lacking on the limbs, and an axillary membrane is present. The tympanum is partially or completely concealed. Males have a single, median, subgular vocal sac and moderately or greatly enlarged prepollices lacking nuptial excrescences. There is a heavy muscular development in the temporal region. The skull is moderately well ossified; a large key-hole shaped frontoparietal fontanelle is present (fig. 149). The sphenethmoid is broad and extends anteriorly between the nasals, which are wide, adjacent to but not sutured to the sphenethmoid, and have moderately long maxillary processes. The quadratojugal is present (*picadoi*) or absent (*zeteki*). The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosal extends about two-fifths of the distance to the maxillary. The medial ramus of the pterygoid is not in bony contact with the prootic. The prevomers do not articulate anteriorly; the dentigerous processes are small and posteromedially inclined. The known tadpoles have moderately long, muscular tails with reduced fins and a dorsal mouth lacking definitive rows of teeth. The mating calls and number of chromosomes are unknown.

COMPOSITION: Two species (*Hyla picadoi* and *zeteki*) comprise the group, which occurs at high elevations in Costa Rica and western Panamá. Forty-seven preserved frogs, two skeletons, and one lot of tadpoles have been examined.

COMMENTS: Although *Hyla picadoi* differs from *zeteki* by having two, instead of one, denticles on the lower jaw, the two species are alike in several characters: broad flat heads with heavy muscular development in the temporal region, granular area around the anal opening, granules above the insertion of the arm, partially or completely concealed tympanum, and greatly reduced webbing between the fingers. This combination of external characters sets these two species apart from other Middle American hylids.

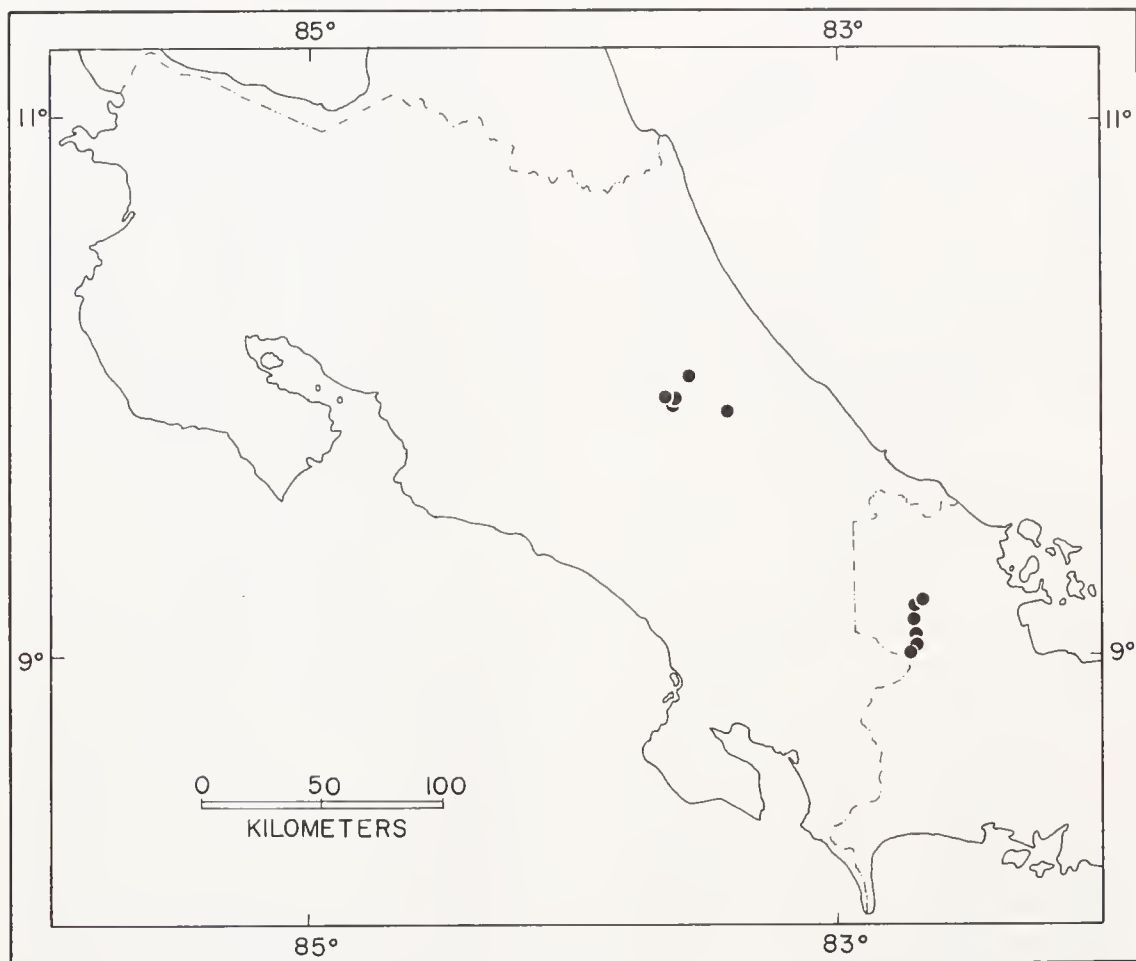


FIG. 148. Distribution of *Hyla lancasteri*.

Hyla zeteki is the only member of the genus in lower Central America known to have tadpoles that develop in bromeliads. Furthermore, it is the only species of Middle American hylids known to have tadpoles with a dorsal mouth. Because *Hyla picadoi* is structurally similar to *zeteki* and because *picadoi* also lives in bromeliads, it is likely that the tadpoles of *picadoi* develop in bromeliads. Tadpoles of *picadoi* and recordings of the mating calls of both species are needed before an assessment of relationships can be made.

No real clues to the relationships of this group to other groups of Middle American *Hyla* are evident. The bromeliad frogs of the *Hyla bromeliacia* group in Mexico and northern Central America evidently are unrelated

to the *zeteki* group. The species in the former group have tadpoles with small ventral mouths and differ from the *zeteki* group in a number of cranial characters. Perhaps the *zeteki* group represents a divergent line from a *Hyla pseudopuma*-like ancestor. Members of the *pseudopuma* group are generalized montane pond breeders in lower Central America.

Hyla picadoi Dunn

Hyla picadoi Dunn, 1937, p. 164 [holotype, M.C.Z. No. 16002 from Volcán Barba, Heredia Province, Costa Rica, 2140 meters; Emmett R. Dunn collector]. Taylor, 1952c, p. 824.

DIAGNOSIS: This moderately small species has a broad head with a heavy muscular development in the temporal region, vestigial

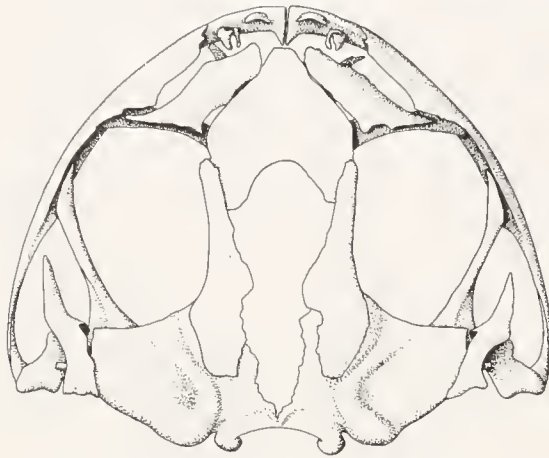


FIG. 149. Dorsal view of the skull of *Hyla picadoi*, K.U. No. 64872. $\times 6$.

webbing on the hands, the toes only about half webbed, granular skin above the insertion of the arm, and the anal opening surrounded by granules. The tympanum is partially or completely concealed. It differs from all other Middle American hylids by having two, instead of one, denticles at the symphysis of the lower jaw. *Hyla picadoi* differs from its apparent closest relative, *H. zeteki*, by its larger size (males to 32.8 mm. in *picadoi* and only to 23.5 mm. in *zeteki*), heavier granular development on ventral surfaces of arms and above the insertion of arms, and in coloration—the lips, loreal region, and supratympanic fold usually are dark in *picadoi*, whereas only the lips are pigmented in *zeteki*.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 32.8 mm., and females reach 35.2 mm. In a series of five males from the highlands of Costa Rica, the snout-vent length is 27.9 to 32.8 (mean, 30.7) mm.; the ratio of tibia length to snout-vent length is 0.463 to 0.527 (mean, 0.501); the ratio of foot length to snout-vent length is 0.419 to 0.464 (mean, 0.436); the ratio of head length to snout-vent length is 0.317 to 0.362 (mean, 0.338); the ratio of head width to snout-vent length is 0.341 to 0.376 (mean, 0.354), and the ratio of the diameter of the tympanum to that of the eye is 0.433 to 0.467 (mean, 0.450).

The head is broader than the body, and the top of the head is flat. In dorsal profile,

the snout is truncate, but pointed terminally; in lateral profile, it is truncate. The snout is short; the nostrils are laterally protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is nearly flat; the lips are moderately thick and barely flared. The temporal region of the head is somewhat expanded. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and on to a point above the insertion of the arm. The fold obscures the upper half of the tympanum, which otherwise is barely discernible or completely concealed beneath the skin. The tympanum is separated from the eye by a distance equal to about three times the length of the tympanum.

The arms are moderately long and robust; an axillary membrane is lacking. No distinct row of tubercles is present on the ventrolateral edge of the forearm, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear moderately large discs; the width of the disc on the third finger is half again the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; the distal tubercle on the fourth finger usually is bifid. The supernumerary tubercles are large, conical, and especially numerous on the proximal segments of each digit. A moderately small, bifid palmar tubercle is present. The prepollex is only moderately enlarged; the extent of a nuptial excrescence in breeding males is not known. The webbing between the fingers is vestigial (fig. 150A). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A heavy transverse dermal fold is present on the heel, and a heavy, glandular tarsal fold extends the full length of the tarsus. Three or four conical tubercles are present on the proximal outer edge of the foot. The inner metatarsal tubercle is elongate and elliptical. The outer metatarsal tubercle is small and subconical. The toes are moderately long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are small and conical, and the super-



FIG. 150. Hands and feet of members of the *Hyla zeteki* group. A and C. *Hyla picadoi*, K.U. No. 65129. B and D. *Hyla zeteki*, K.U. No. 36480. $\times 8$.

numery tubercles are moderately large and subconical. The toes are about two-fifths webbed (fig. 150C). The webbing is vestigial between the first and second toes, and extends from the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs. A granular anal tube is present, and many large granules are present below the anal opening. The skin on the side of the body above the insertion of the arm is weakly granular. The skin on the belly, ventral surfaces of the arms, and proximal posteroventral surfaces of the thighs is strongly granular; elsewhere, the skin is smooth. The tongue is broadly ovoid, emarginate, and barely free posteriorly. The dentigerous processes of the prevomers are narrowly separated, posteromedially inclined elevations between the posterior margins of the small, round choanae. Males have two or three teeth on each process and a total of four to six (mean, 5.3) prevomerine teeth. One adult female has a total of nine prevomerine teeth. A pair of denticles is present at the symphysis of the lower jaw. The vocal slits extend from the midlateral base of the tongue to the angles of the jaw. The vocal sac is single, median, and subgular.

The general coloration of *Hyla picadoi* consists of a yellowish tan dorsum with olive-brown or brown markings (pl. 52, fig. 1). The dorsum usually is nearly uniform yellowish tan or orange-tan; the groin in some individuals has a greenish cast. The belly is white, and the ventral surfaces of the hind limbs and throat are yellow. The iris is reddish copper. The sides of the head and the supratympanic fold usually are pigmented with brown or olive-brown. A dark spot usually is present on the top of the head and sometimes extends posteriorly as an irregular middorsal stripe. The temporal region is orange in many specimens.

One individual (U.S.C. No. 7081) from 1 kilometer southeast of La Chonta, Cartago Province, Costa Rica, had a brown dorsum

with heavy yellow flecking in life; the upper surfaces of the hind limbs were reticulated with brown and yellow. Another individual (U.S.C. No. 668) from El Empalme, Costa Rica, had a metallic golden orange dorsum with an olive cast in life; the head was especially metallic gold (J. M. Savage field notes).

In preservative, the dorsum varies from pale creamy tan to pale brown with scattered brown markings on the side of the head, supratympanic fold, and top of head. In some individuals, faint transverse bands are evident on the dorsal surfaces of the hind limbs. The venter is uniform creamy white, except for a small amount of pigmentation on the ventral surfaces of the feet.

TADPOLES: The tadpoles of *Hyla picadoi* are unknown; possibly they develop in bromeliads.

MATING CALL: No recordings of the call of this species have been obtained; furthermore, the call has not been identified definitely in the field.

NATURAL HISTORY: *Hyla picadoi* is an inhabitant of humid upper montane forests, where the species usually is associated with the bromeliads. Dunn (1937, p. 164) noted that the five specimens available at the time he described the species were all taken from bromeliads on Volcán Barba, Costa Rica. Nine specimens obtained in Costa Rica by J. M. Savage and Norman Scott were all taken from bromeliads; five were obtained in March, and one each in February, June, July, and December.

I obtained three individuals from the Río Poasito on Volcán Poás, Alajuela Province, Costa Rica; one was found on March 21, 1961, and two were obtained on April 17, 1961. All were found on low vegetation near a rocky stream at night. Two individuals were obtained at an elevation of 1920 meters on the north slope of Cerro Pando, Bocas del Toro Province, Panamá, in May, 1966. One juvenile was on a rock in a stream at night, and an adult female was on a bush near the stream at night.

Because individuals were found on vegetation along the streams at night, I suspected that the tadpoles of *Hyla picadoi* probably develop in the stream. Repeated search of the stream along which the frogs had been

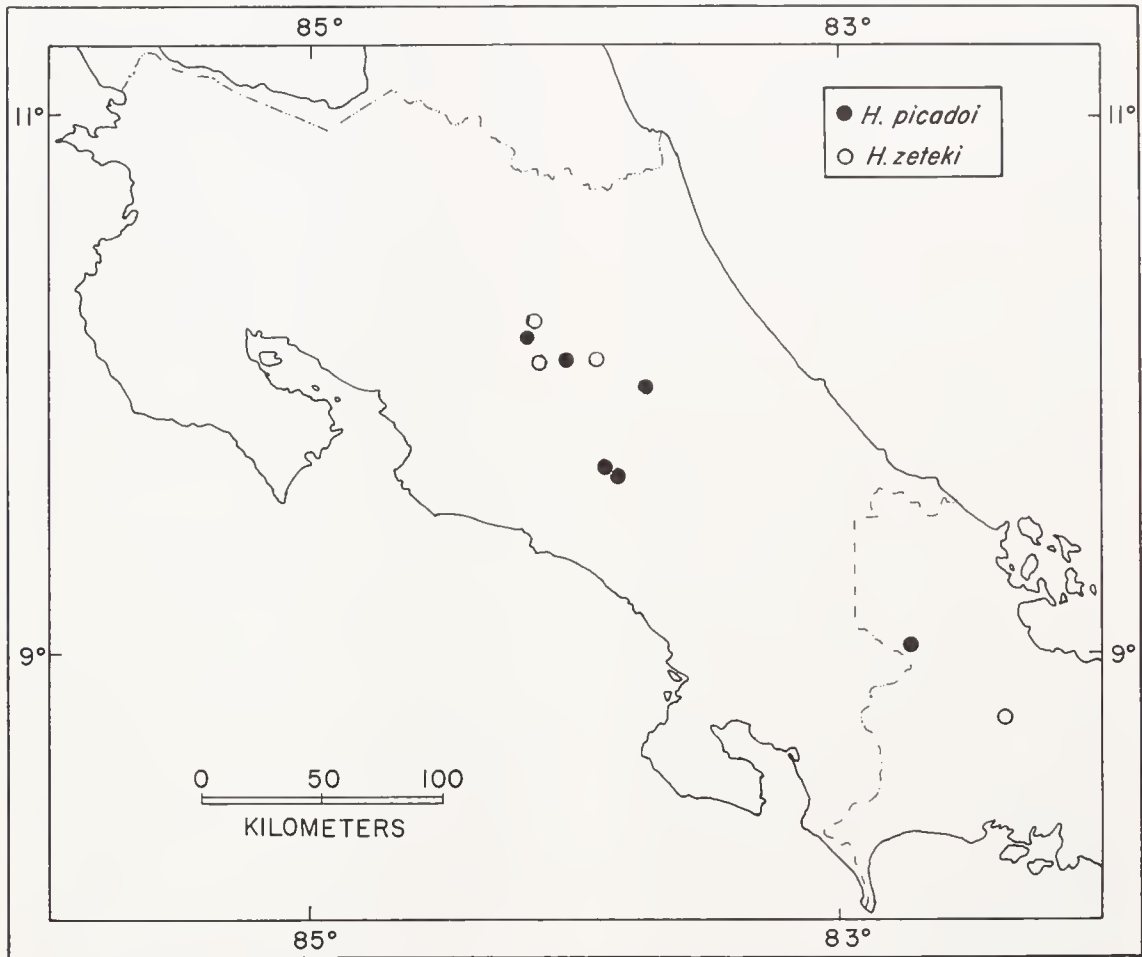


FIG. 151. Distribution of *Hyla picadoi* and *Hyla zeteki*.

found failed to reveal tadpoles that were assignable to *Hyla picadoi*, although tadpoles of the other species of hylids known along the stream were found. Consequently, it does seem probable that tadpoles of *Hyla picadoi*, like those of the related *Hyla zeteki*, develop in bromeliads.

REMARKS: The significance of the paired denticles on the lower jaw is unknown. This is a unique character in *Hyla picadoi*, and is unknown in any other Middle American hylid.

ETYMOLOGY: The specific name is a patronym for C. Picado T., the late Costa Rican naturalist, who contributed greatly to our knowledge of the bromeliad fauna and poisonous snakes of Costa Rica.

DISTRIBUTION: *Hyla picadoi* occurs at high

elevations (1900 and 2510 meters) in the Cordillera Central and Cordillera de Talamanca in Costa Rica and extreme western Panamá (fig. 151). This species occurs at higher elevations than its relative *Hyla zeteki*.

See Appendix 1 for the locality records of the 23 specimens examined.

Hyla zeteki Gaige

Hyla zeteki Gaige, 1929, p. 4 [holotype, U.M.M.Z. No. 63875 from Caldera Valley, above Boquete, Chiriquí Province, Panamá; Helen T. Gaige collector]. Taylor, 1952c, p. 876.

DIAGNOSIS: This small species has a broad head with a heavy muscular development in the temporal region, vestigial webbing on the hands, the toes only about half webbed, granular skin above the insertion of the arm, and

the anal opening surrounded by granules; the tympanum usually is partially concealed. The above combination of characters, plus the general yellowish tan color, will distinguish *Hyla zeteki* from all other Middle American hylids, except *H. picadoi*. The latter is larger (males to 32.8 mm. and only to 23.5 mm. in *zeteki*) and has two denticles instead of one, at the symphysis of the lower jaw. Furthermore, *picadoi* usually has dark pigment on the lips, loreal region, and supratympanic fold, whereas only the lips are pigmented in *zeteki*.

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 23.5 mm., and females reach 26.2 mm. In three adult males from the highlands of Costa Rica and western Panamá, the snout-vent length is 21.3 to 23.5 (mean, 22.5) mm.; the ratio of tibia length to snout-vent length is 0.502 to 0.545 (mean, 0.530); the ratio of foot length to snout-vent length is 0.423 to 0.455 (mean, 0.435); the ratio of head length to snout-vent length is 0.308 to 0.352 (mean, 0.329); the ratio of head width to snout-vent length is 0.339 to 0.362 (mean, 0.352), and the ratio of the diameter of the tympanum to that of the eye is 0.300 to 0.393 (mean, 0.346). In six females from the same region, the snout-vent length is 24.1 to 26.2 (mean, 25.4). The females do not differ significantly from the males in proportions, except that the tympanum is proportionately larger in females. The ratio of the diameter of the tympanum to that of the eye is 0.323 to 0.347 (mean, 0.395).

The head is wider than the body, and the top of the head is flat. The eyes are large and prominent. The snout is broadly rounded in dorsal profile and truncate in lateral profile. The snout is short; the nostrils are barely protruberant at a point about four-fifths of the distance from the eyes to the tip of the snout. The temporal region of the head is somewhat expanded. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward toward the point of insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is barely discernible and separated from the eye by a distance equal to about three times the diameter of the tympanum.

The arms are moderately long and robust; the axillary membrane is absent. There is no row of tubercles on the ventrolateral edge of the forearm, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately short and stout and bear moderately large discs; the width of the disc on the third finger is equal to half again the length of the tympanum. The subarticular tubercles are large and conical; the distal tubercle on the fourth finger and in some individuals on the third finger are bifid. The supernumerary tubercles are large, conical, and especially numerous on the proximal segments of each digit. A low, flat, bifid, palmar tubercle is present. In males the prepollex is greatly enlarged and bulbous, but does not bear nuptial excrescences. The fingers are no more than one-fourth webbed (fig. 150B). The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A weak transverse dermal fold is present on the heel, and a weak tarsal fold extends the full length of the tarsus. Three or four small, low tubercles are present proximally on the outer edge of the foot. The inner metatarsal tubercle is elongate and elliptical. An outer metatarsal tubercle, if present, is low and subconical. The toes are moderately long and slender and bear discs that are nearly as large as those on the fingers. The toes are no more than one-half webbed (fig. 150D). The webbing is vestigial between the first and second toes, and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third, to the base of the antepenultimate phalanx of the fourth, and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs. A heavy, granular anal sheath is present, and a pair of large tubercles is present ventrolaterally on either side of the anal opening. The skin above the insertion of the arm is weakly granular. The skin on the belly, ventral surfaces of the arms, and ventral surfaces of the thighs is strongly granular; elsewhere, the skin is smooth. The tongue is broadly ovoid,

emarginate, and barely free posteriorly. The dentigerous processes of the prevomers are narrowly separated, strongly posteromedially inclined elevations; anterolateral borders of the processes lie between the posterior edges of the small, round choanae. Males have three or four teeth on each process and a total of six to eight (mean, 7.0) prevomerine teeth; females have three to five teeth on each process and a total of seven to nine (mean, 8.0) prevomerine teeth. There is a single denticle at the symphysis of the lower jaw. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla zeteki* is uniform pale yellowish tan (pl. 1, fig. 1). I have not observed *Hyla zeteki* in life. Gaige (1929, p. 5) noted that specimens from Chiriquí Province, Panamá, were "golden tan above becoming iridescent on sides; yellowish white beneath. Iris brownish red. A slender red vertebral stripe and a narrow spectacle-like mark around each eye joining across the snout. In alcohol the red markings have faded and the animal has become a uniform grayish tan." She noted that in a series of 12 specimens the red marks were lacking on the heads in some individuals, but that there was always a trace of red in the coloration. Taylor (1952c, p. 878) in describing a specimen from Isla Bonita, Heredia Province, Costa Rica, noted: "The specimen differs but little in color and marking from the type description. No medium red streak was present or red in the other coloration. The black 'spectacle-like' markings around eyes meeting medially are not clearly defined; the eye is distinctly longer than the snout; the toe discs are smaller than finger discs." Taylor noted that the Costa Rican specimens of *Hyla zeteki* referred to by Dunn (1937, pp. 164-167) differ from the type in the absence of the red dorsal marks as well as the peculiar head markings.

Color notes taken by Dr. J. M. Savage on a specimen (U.S.C. No. 510) from La Palma, San José Province, Costa Rica, are as follows: "Back, arms, legs uniform straw color. Head brownish. Venter whitish. Eyes reddish brown. Undersurface of arms and legs yellowish. Dark line on wrist; brownish on knees.

Brown line from tympanum posterior for a short distance."

In preservative, the frogs are pale creamy tan with no distinctive markings other than a dark line on the wrist and in some specimens a narrow middorsal line anteriorly on the back. In some specimens, the supratympanic fold is lightly pigmented, and in others, especially K.U. No. 36480, the edge of the upper lip is heavily pigmented.

TADPOLES: Dunn (1937, p. 164) provided a brief description of a tadpole of *Hyla zeteki*; Starrett (1960a, p. 26) elaborated on Dunn's description and provided an illustration of the tadpole. The only known lot of tadpoles (A.N.S.P. No. 23822—nine specimens) are now rather soft and faded. For the sake of completeness, I include here another description of these same tadpoles.

A typical tadpole in developmental stage 36 has a body length of 8.1 mm. and a total length of 21.4 mm. The body is depressed and guitar-shaped in dorsal view; the greatest depth of the body is about three-fifths of the greatest width. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is acutely rounded below and interrupted by the mouth dorsally. The eyes are moderately small, not greatly separated medially, and directed dorsolaterally. The nostrils are barely protuberant and situated at a point nearly midway between the eye and the posterior border of the mouth. The opening of the sinistral spiracle is directed posteriorly on the ventrolateral edge of the body at about midlength of the body. The anal tube is long and dextral. The caudal musculature is robust and extends to the tip of the pointed tail. The fins are shallow, deepest posteriorly. The dorsal fin is absent on the anterior one-fourth of the tail (fig. 152).

Dunn (1937, p. 165) commented on the coloration as follows: "... pigmentation of evenly spaced and relatively few melanophores above; fewer and more irregularly spaced below; pale gray with no markings, the white muscles and the color of viscera and foot completely predominated over the pigmentation. . . ." The tadpoles are now pale creamy tan with minute dark flecks on the dorsum and caudal musculature; the fins are unmarked.



FIG. 152. Tadpole of *Hyla zeteki*, A.N.S.P. No. 23822. $\times 5$.

The mouth is anterodorsal and relatively small; its greatest width is equal to about one-third of the greatest width of the body. The mouth is completely bordered by an irregular row of small papillae; the lateral folds in the lips are absent. The beaks extend to the margins of the lips; the lower beak is more massive than the upper one. The upper beak is smooth and the lower beak is finely serrated. A single row of widely separated, short conical teeth is present above the beaks. A lower row is more or less continuous with the single upper row. Medial to the lower row is a secondary shorter row of widely separated teeth (fig. 153).

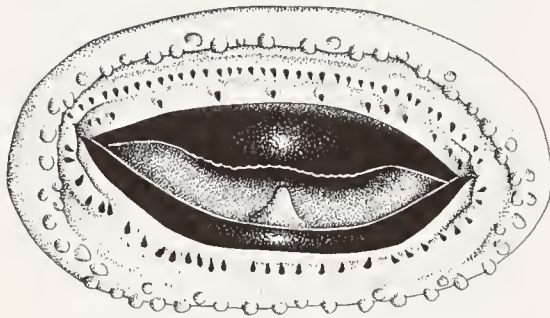


FIG. 153. Mouth of tadpole of *Hyla zeteki*, A.N.S.P. No. 23822. $\times 30$.

Most of the nine specimens are too soft and distorted for accurate measurement. Dunn (1937, p. 165) grouped the tadpoles into four size-groups and noted that the relative length of the tail apparently decreased with age.

MATING CALL: The call of *Hyla zeteki* is unknown.

NATURAL HISTORY: All known specimens of *Hyla zeteki* have been obtained from bromeliads in humid montane forests. Dunn (1937, p. 164) provided evidence that the species breeds in bromeliads. On June 7, 1936, near La Palma, San José Province, Costa Rica, he obtained eggs, tadpoles, and adults from bromeliads. The eggs were found on the out-

side of the leaves above the level of the water. Dunn noted that two eggs were together on the same leaf and that three eggs in another plant were on three separate leaves. The tadpoles were found between the leaves, in the water, but not in the central core of the bromeliads. The stomachs of tadpoles contained only frog eggs. Dunn (1937, p. 166) inferred: "The observed disposition of the five eggs may indicate that *Hyla zeteki* lays its eggs out of water and moves about during oviposition. The stomach contents of the tadpoles may indicate that eggs of its own species furnish the major source of food supply for the tadpoles; the peculiarity of the mouthparts, jaw muscles, and digestive tract may reflect peculiarities of the feeding habits and the food; the reduction of gill filaments may indicate a difference in respiration from more normal hylid tadpoles; the reduction of fin and the progressive reduction of tail lengths may reflect the confined nature of the swimming space."

Taylor (1958, p. 21) noted that a female (K.U. No. 36942) from Varablanca, Cartago Province, Costa Rica, contained numerous, pigmented eggs. Examination of this specimen reveals the presence of 24 large eggs. The number of eggs in this gravid female tends to support Dunn's contention that the females may move about during oviposition.

REMARKS: Both Dunn (1937, p. 165) and Taylor (1952c, p. 878) noted the absence of red markings in Costa Rican specimens, as compared with those from the type locality in western Panamá (Gaige, 1929, p. 5). The lack of sufficient fresh material precludes any assessment of this apparent geographic variation.

ETYMOLOGY: The specific name is a patronym for James Zetek, the former resident-director of Barro Colorado Island in Panamá.

DISTRIBUTION: *Hyla zeteki* occurs at elevations between 1200 and 1800 meters in humid montane forests from central Costa Rica

to western Panamá (fig. 151). The Costa Rican localities are on the Caribbean slopes, whereas the single Panamanian locality for this species is on the Pacific slopes near the Continental Divide.

See Appendix 1 for the locality records of the 27 specimens examined.

The *Hyla bogotensis* Group

DEFINITION: The frogs comprising this group are medium sized stream-breeders; males attain a snout-vent length of 41.8 mm. and females, 48.1 mm. The dorsum is pale green or tan with minute dark flecks or fine reticulations; in some species a pale yellow dorsolateral stripe begins on the canthus and extends to a point above the insertion of the arm. The palpebral membrane is clear; the tympanum is weakly defined or covered. The fingers are about one-third webbed, and the toes are about four-fifths webbed. The tarsal fold is weak, and an axillary membrane is absent. Dermal fringes and appendages are absent on the limbs. A distinct "mental gland" is present on the chin in males (fig. 154), which have a single, median, subgular vocal sac but lack horny nuptial excrescences on the prepollices. The cranial elements are weakly

ossified; a large, key-hole-shaped frontoparietal fontanelle is present. The sphenethmoid is broad but not ossified anteriorly between the nasals, which are wide, have small maxillary processes, barely overlap the sphenethmoid, but are separated medially (fig. 155). The quadratojugal is present. The squamosal is in bony contact with the crista parotica; the anterior arm of the squamosal extends about half of the distance to the maxillary. The medial ramus of the pterygoid does not have a bony articulation with the prootic. The prevomers are only moderately ossified and do not articulate anteriorly; the prevomerine teeth are on anteromedially inclined processes. The tadpoles have moderately long muscular tails and large ventral mouths with six upper and nine lower rows of teeth. The mating call consists of long series of cricket-like chirps. The number of chromosomes is unknown.

COMPOSITION: Four species are currently recognized in this group, which occurs at moderate to high elevations from Costa Rica to Venezuela and Ecuador. Twelve preserved frogs, one skeleton, and three lots of tadpoles have been examined from Middle America.

COMMENTS: *Hyla colymba* is unique among Middle American hylids by having a "mental gland"; furthermore, it is the only species in lower Central America having stream-adapted tadpoles with a multiplicity of tooth rows. Other species having these



FIG. 154. Ventral view of throat of *Hyla colymba*, K.U. No. 95979, showing mental gland. $\times 5$.

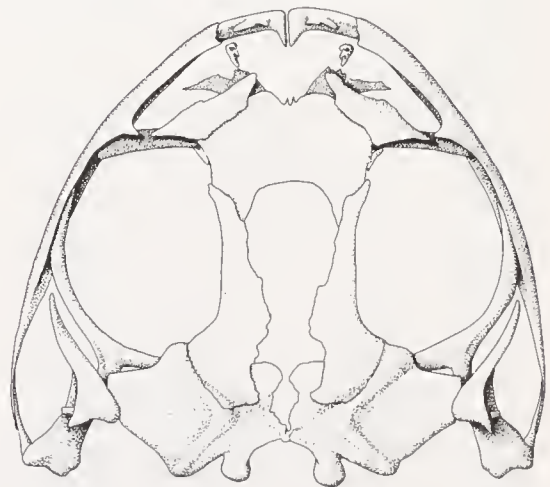


FIG. 155. Dorsal view of skull of *Hyla colymba*, K.U. No. 31865. $\times 5$.

characters are high-elevation species in the northern Andes—*H. bogotensis* (Peters) in Colombia and *H. jahni* Rivero and *H. paramica* Rivero in Venezuela. I have examined the types of all of these nominal species and have examined the sacral diapophyses. The diapophyses are expanded in all, including the type of *Hyla bogotensis*, which Peters (1882a) stated as having rounded diapophyses, a character that he used to erect the genus *Hylo-nomus* (= *Hyloscirtus* Peters, 1882b).

Hyla colymba Dunn

Hyla colymba Dunn, 1931a, p. 400 [holotype, M.C.Z. No. 10234 from La Loma, Bocas del Toro Province, Panamá; Chester Duryea and Emmett R. Dunn collectors]. Duellman, 1966b, p. 267 [synonymized *Hyla alvaradoi* Taylor, 1952c with *Hyla colymba* Dunn, 1931].

Hyla alvaradoi Taylor, 1952c, p. 882 [holotype, K.U. No. 30886 from Moravia, Cartago Province, Costa Rica; Edward H. Taylor collector].

DIAGNOSIS: This moderately small, stream-breeding frog is usually pale green above (capable of changing to pale brown) and bluish green below. A faint creamy yellow line is present on the canthus, edge of upper eyelid, and on the supratympanic fold. In preservative, the dorsum is pale cream with minute dark flecks. The presence of a mental gland immediately distinguishes this frog from all other Middle American hylids. The only other species having similar markings is *Hyla angustilineata*, the juveniles of which have a bright green dorsum, dark brown flanks, and a narrow creamy white dorsolateral line extending to the groin.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 37.0 mm., and females reach 43.3 mm. In six males from Costa Rica and Panamá, the snout-vent length is 31.9 to 37.0 (mean, 34.7) mm.; the ratio of tibia length to snout-vent length is 0.452 to 0.500 (mean, 0.472); the ratio of foot length to snout-vent length is 0.387 to 0.455 (mean, 0.409); the ratio of head length to snout-vent length is 0.302 to 0.325 (mean, 0.316), and the ratio of the diameter of the tympanum to that of the eye is 0.421 to 0.545 (mean, 0.489). Three females from the same area have snout-vent lengths of 31.4 to 39.1 (mean, 36.2) mm. Measurements and proportions of seven males

and five females from Tandapi, Pichincha Province, Ecuador, reveal no significant differences from the Central American sample, except that the females are noticeably larger. The five females have snout-vent lengths of 36.7 to 43.3 (mean, 40.8) mm.

The head is as wide as the body, and the top of the head is flat. The eyes are relatively small and not prominent. In dorsal profile, the snout is acutely rounded; in lateral profile, it is bluntly rounded. The snout is moderately long and shallow; the nostrils are barely protuberant and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is angular, and the loreal region is noticeably concave; the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is only barely distinct and separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and robust; an axillary membrane is absent. There are no tubercles on the ventrolateral edge of the forearm, but a transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear rather small discs; the width of the disc on the third finger is about equal to the diameter of the tympanum. The subarticular tubercles are rather small, round, and elevated; the distal tubercle on the fourth finger is bifid in some individuals. Supernumerary tubercles are lacking; instead, there is a fleshy longitudinal ridge on the proximal segment of each digit. A small, conical palmar tubercle is present. In males, the prepollex is greatly enlarged into an oval structure with a sharp leading edge. The fingers are about one-third webbed (fig. 156A). The webbing is vestigial between the first and second fingers, and extends from the base of the antepenultimate phalanx of the third, from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are rather short and robust; the heels of the adpressed limbs overlap by about one-sixth of the length of the shank. The tibiotarsal articulation extends to the tympanum

or to the posterior edge of the eye. A thin transverse dermal fold is present on the heel, and a low tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, elliptical, and broadly visible from above. An outer metatarsal tubercle is lacking. The toes are moderately short and slender and bear small discs that are barely wider than the penultimate phalanges. The

subarticular tubercles are moderately small and subconical; faint supernumerary tubercles are present distally on some digits, but they are absent proximally. The toes are about four-fifths webbed (fig. 156B). The webbing extends from the middle of the penultimate phalanx of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the distal end of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth, from the middle of the penultimate phalanx of the fourth to the base of the disc of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs. A short anal sheath is present; two vertical folds are present on either side of the anal opening. The skin on the proximal ventral surfaces of the thighs is weakly granular; in some individuals, weak granules are evident on the belly; elsewhere, the skin is smooth. An ovoid "mental gland" is present anteriorly on the chin. All specimens, save one, have this gland. The tongue is elongately ovoid, marginate, and not free posteriorly. The dentigerous processes of the prevomers are elongate, narrowly separated, anteromedially inclined elevations between the posterior margins of the moderately small, elliptical choanae. Individuals of both sexes have five to eight teeth on each process and a total of 11 to 15 (mean, 13.2) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla colymba* is pale green with a faint yellow stripe on the edge of the upper eyelid and on the supratympanic fold (pl. 52, fig. 2). Most individuals when found at night are pale green above with faint yellow flecks or scattered brown dots. A pale yellow stripe begins on the canthus just anterior to the eye or on the edge of the upper eyelid and extends posteriorly along the supratympanic fold usually to a point just above the insertion of the arm. A faint yellow transverse anal stripe is present. In some individuals, a faint creamy yellow line is present on the outer edge of the fore-

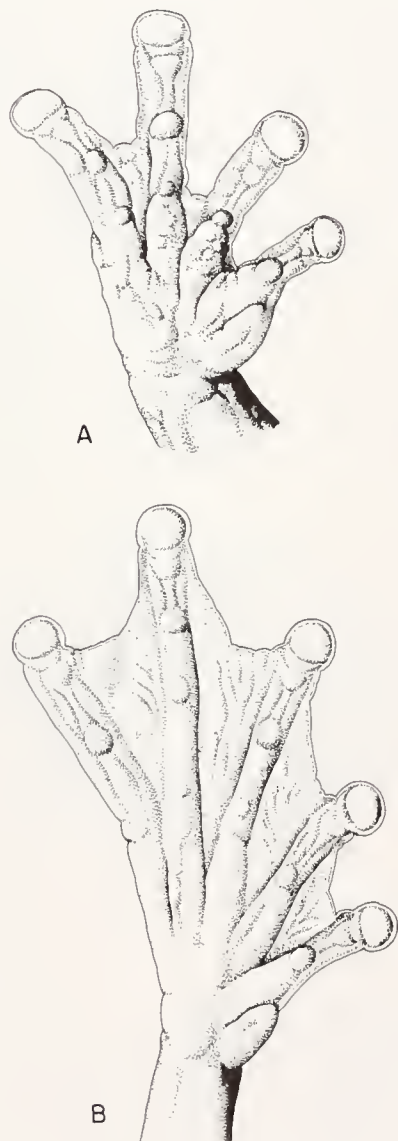


FIG. 156. Hand (A) and foot (B) of *Hyla colymba*, K.U. No. 95979. $\times 5$.

arm and on the outer edge of the foot. The ventral surfaces of the limbs are pale green, and the throat is pale bluish green. The belly and chest are white, and the mental gland is white or creamy yellow. The bones appear pale green through the skin and flesh. The iris is pale brown.

One individual from Laguna, Darién Province, Panamá, was yellowish tan with brown flecks above; the limbs were colored like the dorsum, except that the thighs and upper arms were slightly paler. The anterior part of the head was brown. The mental gland was yellow with brown flecks.

In preservative, the dorsum varies from pale creamy white to creamy tan or pale brown. The short dorsolateral stripes are evident and white. The venter is creamy white. Minute dark flecks are present on the dorsum in many individuals; usually these are most evident on the head and middorsally on the body.

TADPOLES: A typical tadpole in developmental stage 25 has a body length of 15.1 mm. and a total length of 37.3 mm. The body is elongately ovoid, slightly wider than deep. In dorsal profile, the snout is round; in lateral profile, it is acutely rounded. The eyes are small, widely separated, and directed dorso-laterally. The nostrils are situated about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point below the midline and at about midlength of the body. The anal tube is long and dextral. The caudal musculature is robust and terminates just short of the pointed tail. The fins are moderately shallow; at midlength of the tail, the depth of the caudal musculature is greater than the depth of either fin. The dorsal fin does not extend onto the body (fig. 157).

The dorsum of the body is bronze-tan with

golden lichenous flecks. The sides of the body are dark brown with gold flecks. The caudal musculature is tan with dark brown spots; small brown spots are present on the dorsal fin but absent on the ventral fin. The iris is dull bronze. In preservative, the body is brown with faint white flecks. The caudal musculature is creamy tan; brown flecks are present on the musculature and the dorsal fin.

The mouth is ventral and large; its width is equal to about two-thirds of the greatest width of the body. The mouth is completely bordered by two rows of small papillae; deep lateral folds are present in the lips. The beaks are moderately slender and bear rather long, blunt serrations. The upper beak is in the form of a broad arch with long slender lateral processes; the lower beak is broadly V-shaped. There are six upper and nine lower rows of teeth. The sixth upper and first lower rows are narrowly interrupted medially; the other rows are complete. All of the rows are long and extend to the margins of the lip; the three outermost lower rows are somewhat shorter than the others (fig. 158).

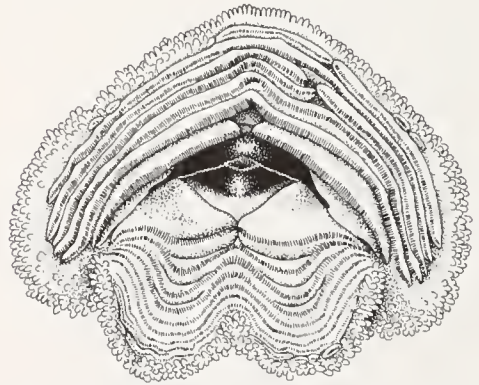


FIG. 158. Mouth of tadpole of *Hyla colymba*, K.U. No. 116779. $\times 15$.



FIG. 157. Tadpole of *Hyla colymba*, K.U. No. 116779. $\times 6$.

The only noticeable variation in the tadpoles of this species is in the number of rows of teeth. In some individuals, a faint seventh upper row is evident; some specimens have only seven or eight lower rows, and one has a short tenth row.

The tadpoles of this species were first described by Dunn (1924, p. 3) as *Hyla albomarginata*; Dunn (1931a, p. 400) later assigned these tadpoles to *Hyla colymba*.

MATING CALL: The call of *Hyla colymba* consists of a series of short, high-pitched, cricket-like chirps. Notes are produced rapidly; the call rate varies from 123 to 236 (mean, 179) notes per minute. There are 12 to 104 notes in each of ten call groups; the interval between call groups varies from one to three seconds. The duration of each note is approximately 0.05 of a second. The fundamental frequency is at about 1800 cycles per second, and the dominant frequency is at about 3600 cycles per second; usually two harmonics above the dominant frequency are evident (pl. 23, fig. 2).

NATURAL HISTORY: *Hyla colymba* inhabits cloud forests or humid lower montane forests, where the frogs have been found only along the streams. Males call from beneath large boulders in small streams. Even in such concealed calling sites, they are extremely wary; at the slightest disturbance, they will cease calling for several minutes. One individual was found on the leaves of a bromeliad at night on Cerro Cituro in the Serranía de Pirre, Darién Province, Panamá. Taylor (1952c, p. 885) noted that a specimen was found on a green plant growing on the edge of a small forest rivulet at Moravia, Cartago Province, Costa Rica. Calling males have been found in the months of April, July, and December.

Tadpoles have been observed in quiet pools in small rocky streams. Dunn (1924, p. 4) noted that he found tadpoles of this species clinging to rocks over which a swift current of water was streaming.

Recently metamorphosed young have been found in April and May; two individuals having completely resorbed tails have snout-vent lengths of 16.9 and 18.7 mm. The juveniles are colored like the adults, except that the hands and feet are yellow. Charles W. Myers observed that the dorsum in juveniles from

Darién Province was sometimes heavily flecked with dark pigment, but at other times this pigment was not visible or was concentrated in small areas.

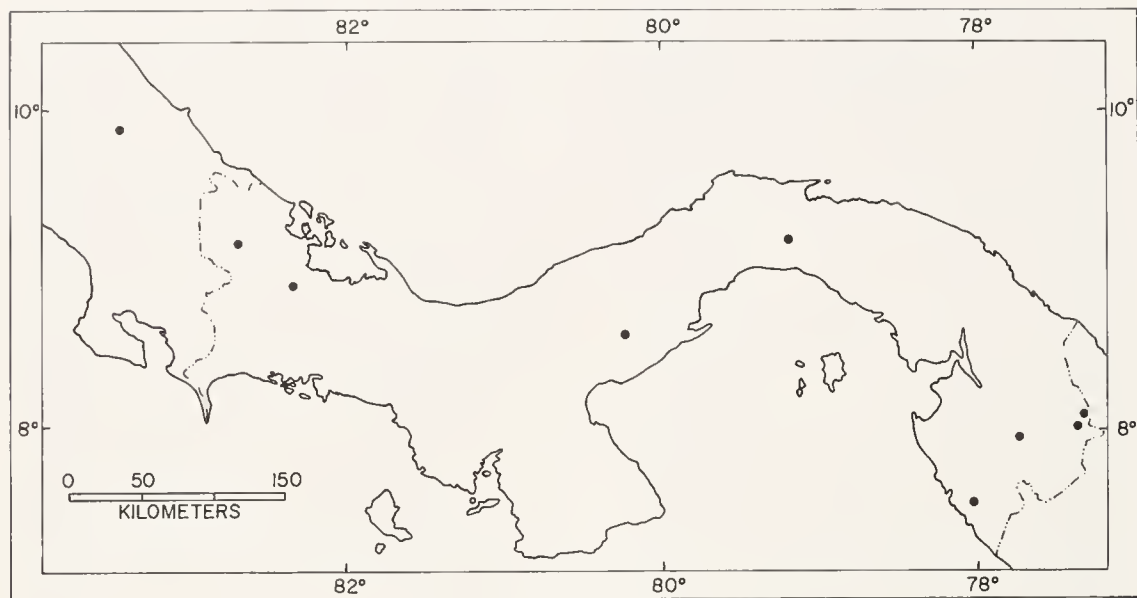
Dunn (1924, p. 3) thought that he might have found the eggs of this species, which he discussed under the name of *Hyla albomarginata*; he stated: "A foamy mass of eggs was found under a rock in the small stream. As this was the situation from which *Hyla albomarginata* was calling, it is quite possible, by association and by elimination of the other three species whose tadpoles inhabited the stream, that these were the eggs of this animal." Dunn also found eggs attached to a leaf overhanging the stream. He thought that these were the eggs of *Hyla uranochiroa*, but since no proof of identity of either clutch of eggs was available, the specific assignment is impossible.

REMARKS: Dunn (1924, p. 3) first obtained this species in the summer of 1923. At that time, he erroneously associated the specimens with *Hyla albomarginata*. He obtained his material at La Loma, Bocas del Toro Province, Panamá. Later Dunn (1931a, p. 400) realized his previously incorrect assignment and named the frogs from La Loma as *Hyla colymba*. Dunn did not mention the mental gland in his description of the species. Taylor (1952c, p. 882) named *Hyla alvaradoi* on the basis of a single adult male from Moravia, Cartago Province, Costa Rica; he gave a detailed description of the holotype and noted the circular mental gland, but he did not compare *Hyla alvaradoi* with *colymba*. Duellman (1966b, p. 267) compared the holotypes of the two species and noted that *alvaradoi* was the same as *colymba*.

In the summer of 1967, a series of adults, juveniles, and tadpoles of this species were obtained at Tandapi, on the Pacific slopes of Ecuador by John D. Lynch. In all essential characters, the adults and larvae from Ecuador are the same as those from Central America. Cochran and Goin (1970) did not record this species from Colombia.

ETYMOLOGY: The specific name is derived from the Greek *kolymbos*, meaning swimmer, and apparently was used in reference to the stream-adapted tadpoles.

DISTRIBUTION: *Hyla colymba* inhabits

FIG. 159. Distribution of *Hyla colymba*.

cloud forests and lower humid montane forests at elevations between 600 and 1400 meters on the Caribbean slopes of Costa Rica and western Panamá and on the Pacific slopes of eastern Panamá (fig. 159). This species also is known from the Pacific slopes of Ecuador and presumably occurs in Colombia.

See Appendix 1 for the locality records of the 16 specimens examined.

The *Hyla salvadorensis* Group

DEFINITION: Members of this group are moderately small stream-breeding species; males attain a maximum snout-vent length of 36.7 mm. and known females, 37.0 mm. The dorsum is dark brown or olive-green without transverse bands on the limbs. The iris is reddish bronze or red, and the palpebral membrane is clear. The hands and feet are large; the hands are about one-half and the feet are about three-fourths webbed. A distinct tarsal fold is present, but an axillary membrane and dermal folds or appendages on the limbs are lacking. Males have single, median, subgular vocal sacs and horny nuptial excrescences on the prepollices. The skull is moderately ossified. A large frontoparietal fontanelle is present. The sphenethmoid extends anteriorly between the nasals, which are moderately slen-

der, widely separated medially, and sutured to the sphenethmoid (*salvadorensis*) or overlap the sphenethmoid (*legleri*). The squamosal is in bony contact with the crista parotica (*salvadorensis*) or not (*legleri*), and the anterior arm of the squamosal extends one-third of the distance to the maxillary (fig. 160). The quadratojugal is present, and the prevomers are moderately well ossified and bear teeth. The medial ramus of the

FIG. 160. Dorsal view of the skull of *Hyla salvadorensis*, K.U. No. 103033. $\times 6$.

pterygoid is in bony contact with the prootic. The tadpoles have long muscular tails and ventral mouths with two or three upper and five lower rows of teeth. The mating calls consist of a single long, or a series of short, poorly modulated notes. The haploid number of chromosomes is 12.

COMPOSITION: Two species (*Hyla legleri* and *salvadorensis*) comprise the group, which occurs at moderate elevations on the Pacific slopes from El Salvador to western Panamá. Eighty-one preserved frogs, five skeletons, and nine lots of tadpoles have been examined.

COMMENTS: *Hyla legleri*, formerly associated with the *Hyla uranochroa* group because of its red eyes, seems to be more closely allied to *Hyla salvadorensis*. Members of the *Hyla uranochroa* group have noticeably different skulls and tadpoles from those of *legleri*, which are like those of *salvadorensis*.

In frogs of the *Hyla uranochroa* group, the bright red color of the iris develops early in larval development (present in developmental stage 25). The same is true of *Hyla erythromma* in México. In *Hyla legleri* the iris in the young tadpoles is deep bronze, and the red pigment is not apparent until developmental stage 38 or 39; the red pigment does not fully develop in *salvadorensis*.

The two species in this group inhabit montane areas and probably represent relicts of a former population that was widespread from Costa Rica northward across the Nicaraguan gap to the highlands of Nuclear Central America (highlands of Chiapas, Guatemala, and Honduras).

Hyla legleri Taylor

Hyla legleri Taylor, 1958, p. 33 [holotype, K.U. No. 32932 from 15 kilometers west-southwest of San Isidro el General, San José Province, Costa Rica; Edward H. Taylor collector].

DIAGNOSIS: This moderately small species has a dark reddish brown or olive-green dorsum, a white lateral stripe, a distinct white anal stripe, white stripes along the outer edges of the forearms and feet, a red eye, and a dark gray vocal sac in breeding males. It differs from its close relative, *Hyla salvadorensis*, by having smaller discs and pale brown or yellowish tan, instead of dark brown, on the posterior surfaces of the thighs. Furthermore,

salvadorensis has a coppery-bronze colored eye and lacks well-defined white stripes. *Hyla uranochroa* and *rufioculis*, both of which have red eyes, differ from *legleri* by being smaller and by having more truncate snouts, less webbing, pale throats in breeding males and a distinct white labial stripe. The other red-eyed Middle American species, *erythromma*, differs by having a pale green dorsum and a faintly reticulated palpebral membrane.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 36.7 mm., and females reach 37.0 mm. In a series of 18 males from the Pacific slopes of Costa Rica, the snout-vent length is 31.7 to 36.7 (mean, 33.5) mm.; the ratio of tibia length to snout-vent length is 0.462 to 0.509 (mean, 0.485); the ratio of foot length to snout-vent length is 0.407 to 0.443 (mean, 0.425); the ratio of head length to snout-vent length is 0.307 to 0.360 (mean, 0.339); the ratio of head width to snout-vent length is 0.312 to 0.358 (mean, 0.343), and the ratio of the diameter of the tympanum to that of the eye is 0.459 to 0.618 (mean, 0.534). Three females from the same areas have snout-vent lengths of 36.0 to 37.0 (mean, 36.5) mm. and do not differ significantly in proportions from the males.

The head is as wide as the body, and the top of the head is barely convex. In dorsal profile, the snout is acutely rounded; in lateral profile, it is rounded above and terminally truncate. The snout is moderately long; the nostrils are barely protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is weakly angular; the loreal region is flat, barely inclined, and the lips are moderately thick and barely flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately short and robust. An axillary membrane is absent. A row of tubercles, which in some specimens are fused into a low, thick dermal fold, extends the length of the ventrolateral edge of the forearm; a weak transverse dermal fold is present

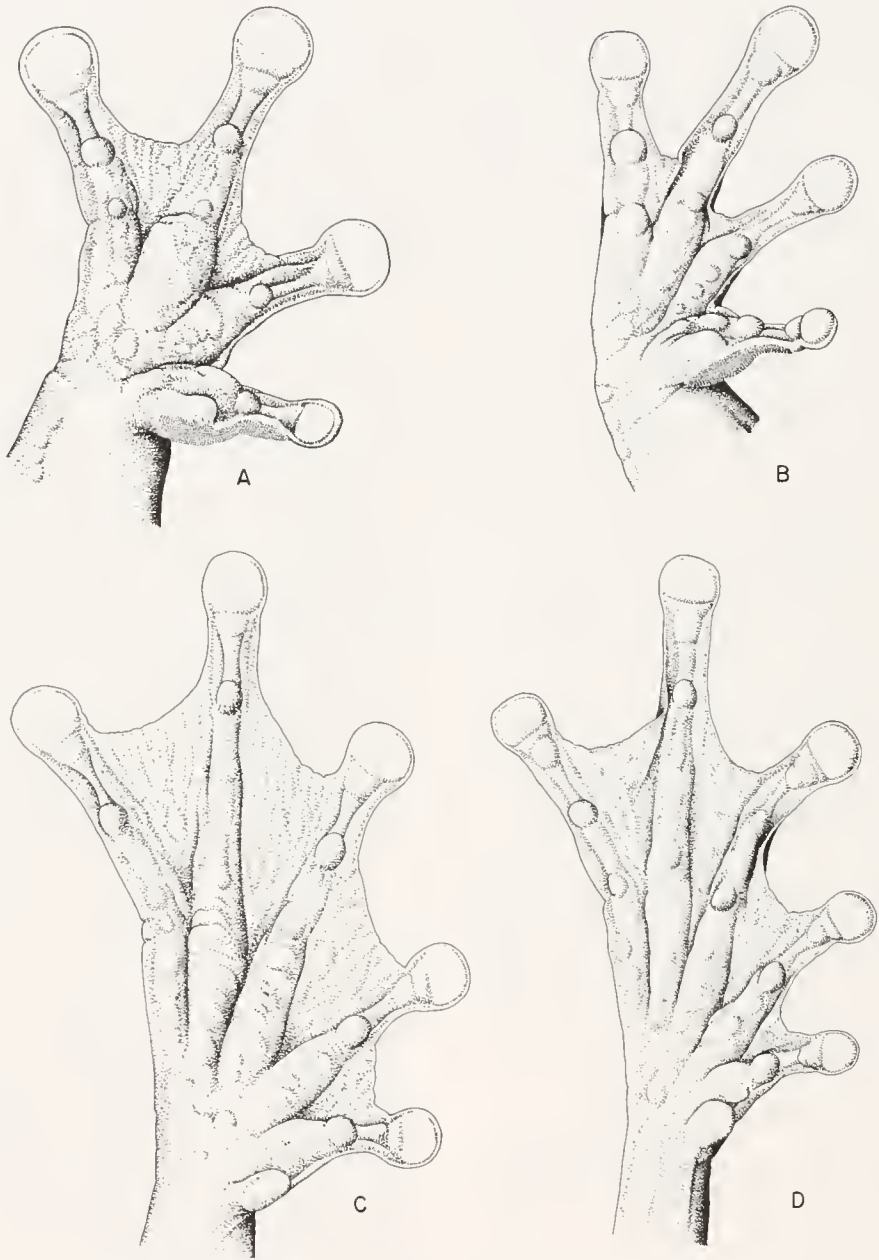


FIG. 161. Hands and feet of members of the *Hyla salvadorensis* group. A and C. *Hyla legleri*, K.U. No. 103685. B and D. *Hyla salvadorensis*, K.U. No. 103256. $\times 5$.

on the wrist. The fingers are rather short and stout and bear large discs; the width of the disc on the third finger is equal to the diameter of the eye. The subarticular tubercles are large and round; in a few specimens, the distal tubercle on the fourth finger is weakly

bifid. The supernumerary tubercles are low and indistinct. A low, bifid palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about one-half webbed (fig. 161A). The webbing is

vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third and on to the middle of the penultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fifth of the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A weak dermal fold is present on the heel, and a low tarsal fold is present on the distal half of the tarsus. The inner metatarsal tubercle is low, flat, ovoid, and barely visible from above. No distinct outer metatarsal tubercle is present. The toes are moderately long and stout and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are moderately large and round, and the supernumerary tubercles are low and indistinct. The feet are about three-fourths webbed (fig. 161C). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. A short, broad anal sheath is present, and numerous small tubercles are present below the anal opening. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is broadly cordiform, shallowly notched behind, barely notched anteriorly in some specimens, and not free posteriorly. The denticulous processes of the prevomers are small transverse elevations between the moderately small, ovoid choanae. Males have three or four (mean, 3.6) teeth on each process, and females have four or five (mean, 4.7) teeth on each process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla legleri* is dark brown above and creamy white below

(pl. 54, fig. 5). The dorsum usually is some shade of brown, either olive-brown or dull reddish brown. In some individuals, darker reticulations of olive-brown or reddish brown are visible on the dorsum. A creamy yellow stripe extends the length of the flank and is not continuous with a thin white stripe on the upper lip, which is absent in some specimens. The anterior and posterior surfaces of the thighs are orange-brown to yellowish tan. There are no transverse bands on the limbs. A distinct white stripe is present above the anal opening and on the ventrolateral edges of the forearms and feet. The posterior surface of the upper arm proximally is white. The belly is creamy white, and the throat in breeding males is dark gray. The iris is red.

In preservative, the dorsum varies from dull reddish brown to dark brown. The anterior and posterior surfaces of the thighs are pale reddish brown to creamy tan. The stripe on the lip, flanks, forearms, feet, and above the anus are creamy white. Usually the tubercles below the anal opening are tipped with white. The ventral surfaces are creamy tan, except the throat, which is dark gray or heavily suffused with brown in breeding males.

TADPOLES: A developmental series of tadpoles is available from 15 kilometers west-southwest of San Isidro el General, San José Province, Costa Rica (table 36). A typical tadpole in developmental stage 36 has a body length of 14.0 mm. and a total length of 41.0 mm. The body is ovoid, widest anteriorly, and somewhat wider than deep. In dorsal profile, the snout is bluntly rounded, and in lateral profile, it is acutely rounded. The eyes are large, widely separated, and directed dorso-laterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The sinistral spiracle is rather small and situated below the midline at about midlength of the body. The anal tube is short and dextral. The caudal musculature is robust and extends nearly to the tip of the rounded tail. The fins are relatively low, and the dorsal fin does not extend on to the body. At midlength of the tail, the depth of the caudal musculature is greater than the depth of either the dorsal or ventral fins (fig. 162A).



FIG. 162. Tadpoles of members of the *Hyla salvadorensis* group. A. *Hyla legleri*, K.U. No. 104138. B. *Hyla salvadorensis*, K.U. No. 68497. $\times 3$.

The body and tail are pale tan with dark brown flecks and spots; the latter tend to form transverse bands on the dorsal surface of the tail. The venter is creamy white. The iris is bronze in earlier developmental stages; in stage 38 or 39, the iris begins taking on a reddish appearance. In preservative, the body and tail are pale creamy tan with brown flecks and blotches. Few, if any, flecks are present on the ventral fin.

The mouth is ventral and moderately large; its width is equal to slightly more than the greatest width of the body. Deep lateral folds are present in the lips which are completely bordered by two rows of small papillae; additional papillae are present in the lateral folds. The beaks are moderately well developed and bear short, blunt serrations. The upper beak is in the form of a broad arch with moderately robust lateral processes; the lower beak is

broadly V-shaped. There are two or three upper rows of teeth and five lower rows. The third upper row, when present, is composed of small teeth arranged in a fragmented row at the inner edge of the papillae. The first, and sometimes the second upper row is narrowly interrupted medially. The lower rows are complete and nearly as long as the upper rows (fig. 163A).

MATING CALL: The call of *Hyla legleri* consists of a single, moderately long, poorly modulated note. An analysis of eight recordings reveals that the note repetition rate varies from eight to 32 (mean, 14) notes per minute. The duration of each note is 0.23 to 0.40 (mean, 0.29) of a second, and the pulse rate is 89 to 125 (mean, 108) pulses per second. The fundamental frequency varies from 83 to 230 (mean, 149) cycles per second. Two frequencies usually are emphasized. The low-

TABLE 36
Measurements of Tadpoles of *Hyla legleri*, with Means in Parentheses,
in Relation to Developmental Stages.

Stage	N	Body Length	Tail Length	Total Length
25	13	6.5-11.9 (9.24)	11.5-24.8 (16.9)	18.0-36.2 (26.2)
26	2	10.9-11.8 (11.3)	18.9-21.8 (20.4)	29.8-33.6 (31.7)
28	2	10.9-12.6 (11.8)	23.3-27.0 (25.2)	34.2-39.6 (36.9)
30	3	12.6-13.2 (12.8)	24.1-28.1 (25.9)	36.8-40.7 (38.7)
31	3	12.8-13.7 (13.2)	24.9-28.3 (26.2)	37.7-42.0 (39.4)
36	5	13.0-14.9 (13.9)	26.8-30.2 (28.7)	40.2-44.9 (42.7)
40	4	13.2-14.5 (14.1)	27.8-32.0 (30.9)	41.0-44.9 (44.8)
42	3	14.3-14.6 (14.5)	28.2-31.2 (28.9)	42.5-45.8 (43.4)
46	4	14.6-18.1 (15.9)	-----	-----

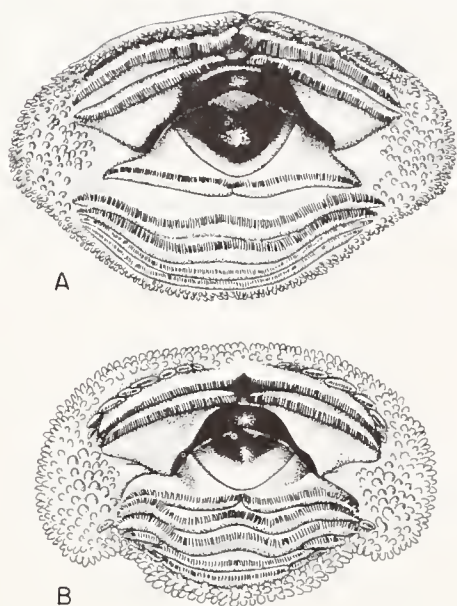


FIG. 163. Mouths of tadpoles of the *Hyla salvadorensis* group. A. *Hyla legleri*, K.U. No. 104138. B. *Hyla salvadorensis*, K.U. No. 68497. $\times 12$.

er of these is between 1036 and 1427 (mean, 1274) cycles per second, whereas the upper is between 2036 and 2745 (mean, 2397) cycles per second (pl. 22, fig. 3).

NATURAL HISTORY: *Hyla legleri* inhabits humid montane forests, where this species usually is found along small streams. Males have been heard calling from February through July. Males usually call from dense vegetation no more than 1 meter above the water. Some calling males have been found on rocks in the stream when these rocks are covered by dense vegetation.

The tadpoles develop in shallow streams, where they live in those parts of the stream having a gravel bottom and subject to moderate currents. The coloration of the tadpoles blends well with the color of the stream bottom, so that the tadpoles are difficult to see. When disturbed, the tadpoles swim away to rest again on the bottom; they do not actually seek shelter beneath rocks or amidst debris in the stream.

Recently metamorphosed young have been found in May and July. The young are dull olive-green above and white below. The white stripe and mark present in adults are obvious

in the juveniles; in addition, the heels and elbows in juveniles are marked with white. These recently metamorphosed young have bright red eyes.

REMARKS: Taylor (1958, p. 37) in his description of *Hyla legleri* suggested that the new species was related to *Hyla nigripes* Cope (= *Smilisca sordida* Peters). Subsequent workers, such as Starrett (1966) and Duellman (1966b) considered *Hyla legleri* to be allied with the other Costa Rican red-eyed species (*Hyla rufoculis* and *uranochroa*). On the basis of the cranial osteology of the adult and the characteristics of the tadpoles, I now place *Hyla legleri* in close association with *Hyla salvadorensis* and consider that the species is not closely related to *Hyla rufoculis* and *uranochroa*.

ETYMOLOGY: The specific name is a patronym for Dr. John M. Legler, a former curatorial assistant at the Museum of Natural History at the University of Kansas.

DISTRIBUTION: *Hyla legleri* occurs at elevations between 700 and 1600 meters on the Pacific slopes of the Cordillera de Talamanca in eastern Costa Rica and extreme western Panamá (fig. 164).

See Appendix 1 for the locality records of the 65 specimens examined.

Hyla salvadorensis Mertens

Hyla salvadorensis Mertens, 1952a, p. 169 [holotype, S.N.M. No. 43045 from Hacienda San José, Sierra Metapán, Departamento Santa Ana, El Salvador; Robert Mertens collector].

Ptychohyla spinipollex (in part): Lynch and Fugler, 1965, p. 11.

DIAGNOSIS: This moderately small species has a dull brown dorsum and posterior surfaces of the thighs, faint white stripes on the outer edges of the forearms and feet and above the anus, mottled flanks, a coppery bronze iris, and a dusky throat in breeding males. *Hyla legleri* differs by having a red eye, well-defined white stripes on the outer edges of the forearms and feet and above the anus, a white lateral stripe, and larger discs. Superficially, *Hyla salvadorensis* is similar to *Ptychohyla euthysanota* and *spinipollex*; the latter have bronze-colored eyes and in breeding males large ventrolateral glands and nuptial excrescences composed of spines, instead of

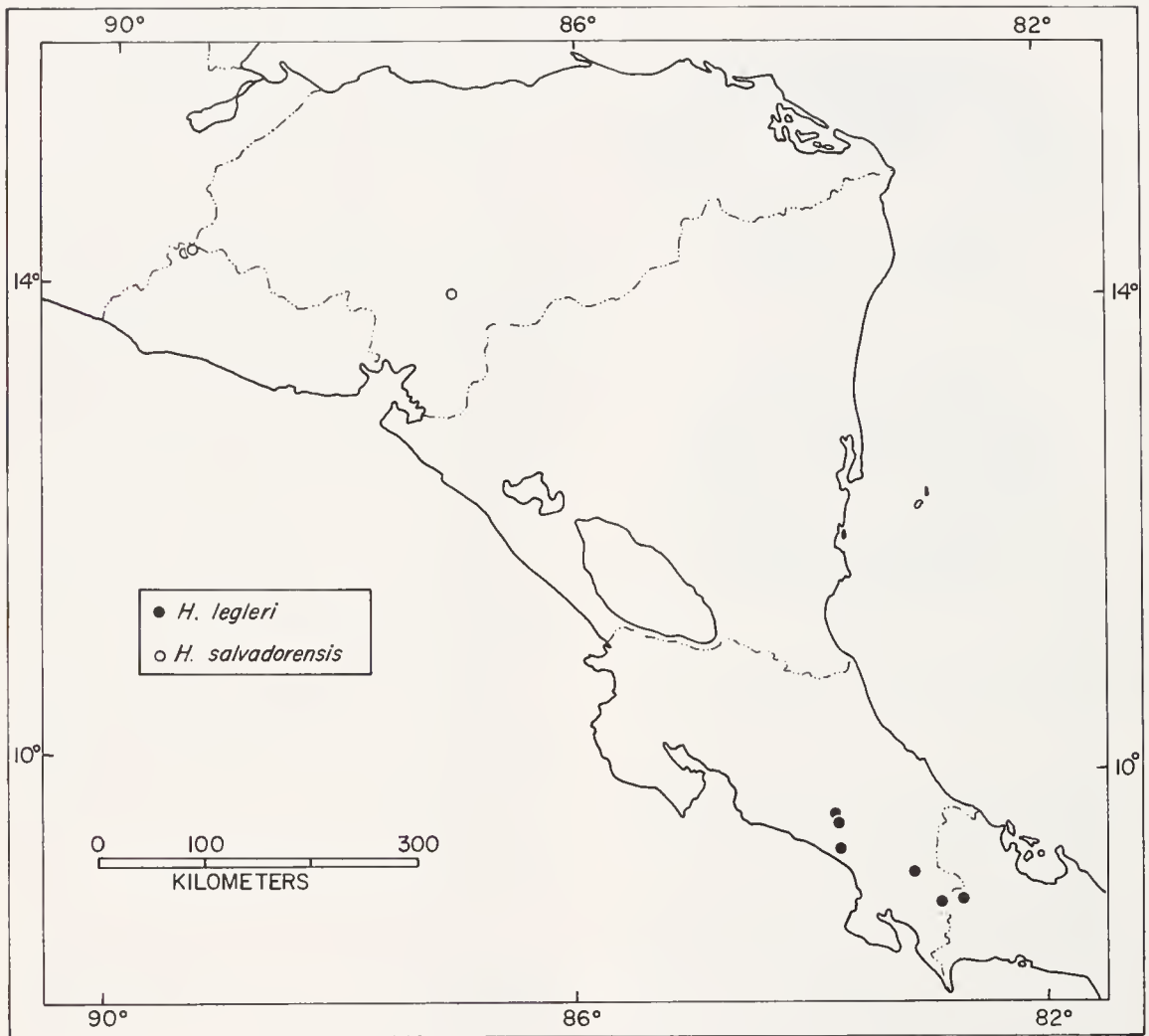


FIG. 164. Distribution of *Hyla legleri* and *Hyla salvadorensis*.

a horny pad. Furthermore, *P. spinipollex* has a vertical rostral keel and bold mottling on the flanks.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 35.9 mm.; adult females are unknown.⁵ In a series of six males from Cerro Uyuca, Departamento Francisco-Morazán, Honduras, the snout-vent length is 34.3 to 35.9 (mean, 34.9) mm.; the ratio of tibia length to snout-vent length is 0.471 to 0.520 (mean,

0.491); the ratio of foot length to snout-vent length is 0.390 to 0.410 (mean, 0.400); the ratio of head length to snout-vent length is 0.315 to 0.341 (mean, 0.330); the ratio of head width to snout-vent length is 0.319 to 0.353 (mean, 0.337), and the ratio of the diameter of the tympanum to that of the eye is 0.556 to 0.625 (mean, 0.590). Three males from the Pacific slope in El Salvador have snout-vent lengths of 30.5 to 31.6 (mean, 31.1) mm. and do not differ in proportions from the specimens from Cerro Uyuca.

The head is as wide as the body, and the top of the head is barely convex. In dorsal profile, the snout is acutely rounded, and in

⁵ Dr. John R. Meyer obtained a gravid female having a snout-vent length of 41.1 mm. on June 28, 1968, at 14.4 kilometers east of Nueva Ocotepeque, Departamento de Ocotepeque, Honduras.

lateral profile, it is round. The snout is moderately long; the nostrils are barely protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is barely concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and on to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately short and robust; an axillary membrane is absent. A row of low tubercles on the ventrolateral edge of the forearm is fused into a nearly continuous fold; a weak transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear medium-sized discs; the width of the disc on the third finger is equal to about two-thirds of the diameter of the tympanum. The subarticular tubercles are moderately large and round; the distal tubercle on the fourth finger is weakly bifid in some specimens. The supernumerary tubercles are low and indistinct. The palmar tubercle is large, ovoid, and usually entire. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about one-third webbed (fig. 161B). The webbing is vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third and from the distal end of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and robust. The heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the posterior corner of the eye. A transverse dermal fold is present on the heel, and a weak tarsal fold is present distally on the tarsus. The inner metatarsal tubercle is low, flat, ovoid, and not visible from above. The outer metatarsal tubercle is minute and conical. The toes are moderately short and stout and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moder-

ately large and round and the supernumerary tubercles are low and indistinct. The toes are about two-thirds webbed (fig. 161D). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. A short, broad anal sheath is present, but tubercles are absent below the anal opening. The skin on the throat, belly, and ventral surfaces of the thighs is granular; elsewhere the skin is smooth. The tongue is broadly cordiform, shallowly notched posteriorly and barely, if at all, free behind. The dentigerous processes of the prevomers are small, widely separated, transverse ridges between the moderately large, ovoid choanae. Males have three to five (mean, 4.3) teeth on each process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla salvadorens* is dull brown above and creamy white below (pl. 59, fig. 4). At night, specimens from Cerro Uyuca were pale olive-gray or pale tan with faint olive-brown markings above. By day, the dorsum changed to brown with darker brown markings with or without small yellow flecks. The anterior and posterior surfaces of the thighs, the ventral surfaces of the legs, the first three toes, and the thumb are orange-brown. The chin and chest are white, and the belly is pale creamy yellow, becoming pale orange posteriorly. The flanks are mottled silvery white and dark brown. The edge of the chin is heavily flecked with dark brown in breeding males. There is a narrow white stripe on the upper lip, on the outer edge of the forearm and foot, and above the anus. The iris is a copper color with fine black flecks. Individuals from Rancho San José, Departamento Santa Ana, El Salvador, were dull green above with darker olive-green

markings. Otherwise, they were colored like those from Cerro Uyuca.

In preservative the dorsum is dull brown with faint darker brown flecks and fine reticulations; there are no distinct transverse marks on the limbs. The anterior and posterior surfaces of the thighs are pale brown or yellowish tan. The venter is pale creamy tan with grayish brown flecks on the periphery of the chin. The flanks are brown with white flecks or mottling. A thin, frequently interrupted, white stripe is present on the very edge of the upper lip. The white strip on the outer edges of the forearms and feet are narrow, but distinct. In most specimens a narrow, but distinct, white line is present above the anus.

TADPOLES: A small series of tadpoles is available from Rancho San José, Departamento Santa Ana, El Salvador. Five tadpoles in developmental stage 25 have body lengths of 13.5 to 14.2 (mean, 13.9) mm. and total lengths of 39.5 to 42.3 (mean, 41.3) mm. Two tadpoles in developmental stage 38 each have a body length of 16.0 mm. and a total length of 48.0 mm.

A typical tadpole in developmental stage 25 has a body length of 14.0 mm. and a total length of 42.0 mm. The body is ovoid, widest at midlength, and only slightly wider than deep. In dorsal profile, the snout is bluntly rounded, and in lateral profile it is round. The eyes are moderately large, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point just below the midline slightly posterior to the midlength of the body. The anal tube is short and dextral. The caudal musculature is robust and extends nearly to the tip of the rounded tail. The fins are low, and the dorsal fin does not extend onto the body. At midlength of the tail, the depth of the caudal musculature is much greater than the depth of either the dorsal or ventral fins (fig. 162B).

In preservative, the body is dull brown; the caudal musculature is creamy tan and the caudal fins are transparent. The tail is marked by numerous interconnecting brown flecks and streaks.

The mouth is ventral and moderately

large; its width is equal to slightly more than one-half of the greatest width of the body. Deep lateral folds are present in the lips, which are completely bordered by two rows of small papillae; numerous additional papillae are present in the lateral folds. The beaks are well developed and bear short, blunt serrations. The upper beak is in the form of a broad arch with moderately long, robust lateral processes. The ventral beak is broadly V-shaped. There are two or three upper rows and five lower rows of teeth. The first upper row is narrowly interrupted medially, and the third upper row is fragmentary. The upper rows are about equal in length and somewhat longer than the lower rows, all of which are entire and progressively shorter (fig. 163B).

MATING CALL: The call of *Hyla salvadorensis* consists of a short series of short notes. Call groups consist of two to six notes; the duration of each call group varies from 0.27 to 0.78 (mean, 0.38) of a second, and the duration of the notes varies from 0.05 to 0.12 (mean, 0.083) of a second. There are two distinct pulses in each note. The notes are poorly modulated; the dominant frequency varies from 2200 to 2700 (mean, 2345) cycles per second (pl. 22, fig. 2).

Recordings obtained at Cerro Uyuca, Honduras, revealed that the frogs there produced only two notes in each call group, where frogs at Rancho San José, El Salvador, produced from three to six notes in each call group.

NATURAL HISTORY: *Hyla salvadorensis* inhabits cloud forests and pine forests, where this species most frequently is encountered along small streams. Males were found calling on Cerro Uyuca on July 5, 1966, and at Rancho San José on July 27, 1961. At both places, the frogs called from dense vegetation over the streams.

Tadpoles were found on July 21, 1961, at Rancho San José. There the tadpoles inhabited quiet pools in a rocky stream.

REMARKS: Fourteen specimens (A.M.N.H. Nos. 54823 and 54827-54839) from Cerro Uyuca, Honduras, are poorly preserved. Lynch and Fugler (1965, p. 6) erroneously referred these specimens to *Ptychohyla spinipollex*.

ETYMOLOGY: The specific name refers to

the country of El Salvador, from which the first specimens were taken.

DISTRIBUTION: *Hyla salvadorensis* occurs at elevations between 700 and 1870 meters on the Pacific slopes of the highlands in northern El Salvador and south-central Honduras (fig. 164).

See Appendix 1 for the locality records of the 30 specimens examined.

The *Hyla miliaria* Group

DEFINITION: The members of this group are moderately large to large species; males attain a maximum snout-vent length of 106 mm. The dorsum is green or tan mottled or not with brown or dark green. The palpebral membrane is clear or pigmented ventrally. The hands and feet are immense, and the discs are large. The fingers are at least two-thirds webbed, and the toes are more than three-fourths webbed. Scalloped dermal fringes are present on the outer edge of the forearm and fourth finger and on the outer edge of the foot and fifth toe. The dorsum is tuberculate in known juveniles and smooth or tuber-

culate in adults. Males have single, median, subgular vocal sacs and the prepollex variously modified as a projecting spine, spade-like plate or clump of spines. The skull is moderately well ossified; an elongate frontoparietal fontanelle is present, and in some species, the skin is co-ossified with the frontoparietals and squamosals. The frontoparietals are expanded laterally over the orbits (fig. 165). The sphenethmoid is broad and extends anteriorly between the nasals, which are greatly reduced. The quadratojugal is in bony contact with the maxillary, and the median ramus of the pterygoid is in bony contact with the prootic. The anterior arm of the squamosal extends no more than one-half of the distance to the maxillary. The prevomers are reduced and bear transverse or antero-medially inclined dentigerous processes. The palatines are slender. The tadpoles, mating calls, and chromosome numbers are unknown.

COMPOSITION: Five species (*H. echinata*, *fimbrimembra*, *miliaria*, *thysanota*, and *valancifer*) comprise the group. Fourteen preserved frogs, plus one from South America, were examined, and skulls were removed from two specimens.

COMMENTS: Firschein and Smith (1956) and Duellman (1962) considered the Middle American fringe-limbed *Hyla* to be members of the *Hyla tuberculata* group. Boulenger (1882a) named *Hyla tuberculata* on the basis of a single female having a snout-vent length of 67 mm. from Amazonian Ecuador.

So few specimens of these bizarre frogs are known that adequate comparisons between species are not possible; adult males of *fimbrimembra* and *thysanota* have yet to be found. The absence of tadpoles and recordings of mating calls further hinders meaningful suggestions of relationships. Solely on the basis of the external morphology of the adults, I think that *echinata* and *valancifer* are closely related and less specialized than the other species; possibly *fimbrimembra* should be placed with those two species, but *fimbrimembra* has the skin on the skull partially co-ossified. *Hyla thysanota* and *miliaria* have the largest feet and best developed dermal fringes and thereby seem to be the most advanced species (figs. 166-168).

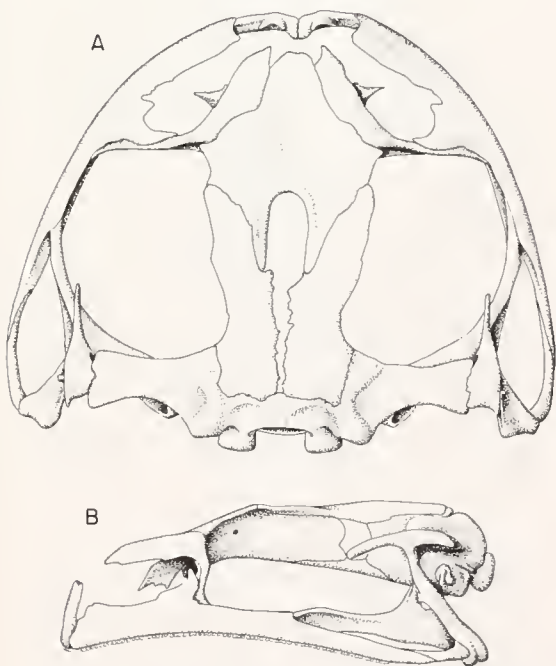


FIG. 165. Dorsal (A) and lateral (B) views of the skull of *Hyla valancifer* (K.U. No. 95416). $\times 2.5$.

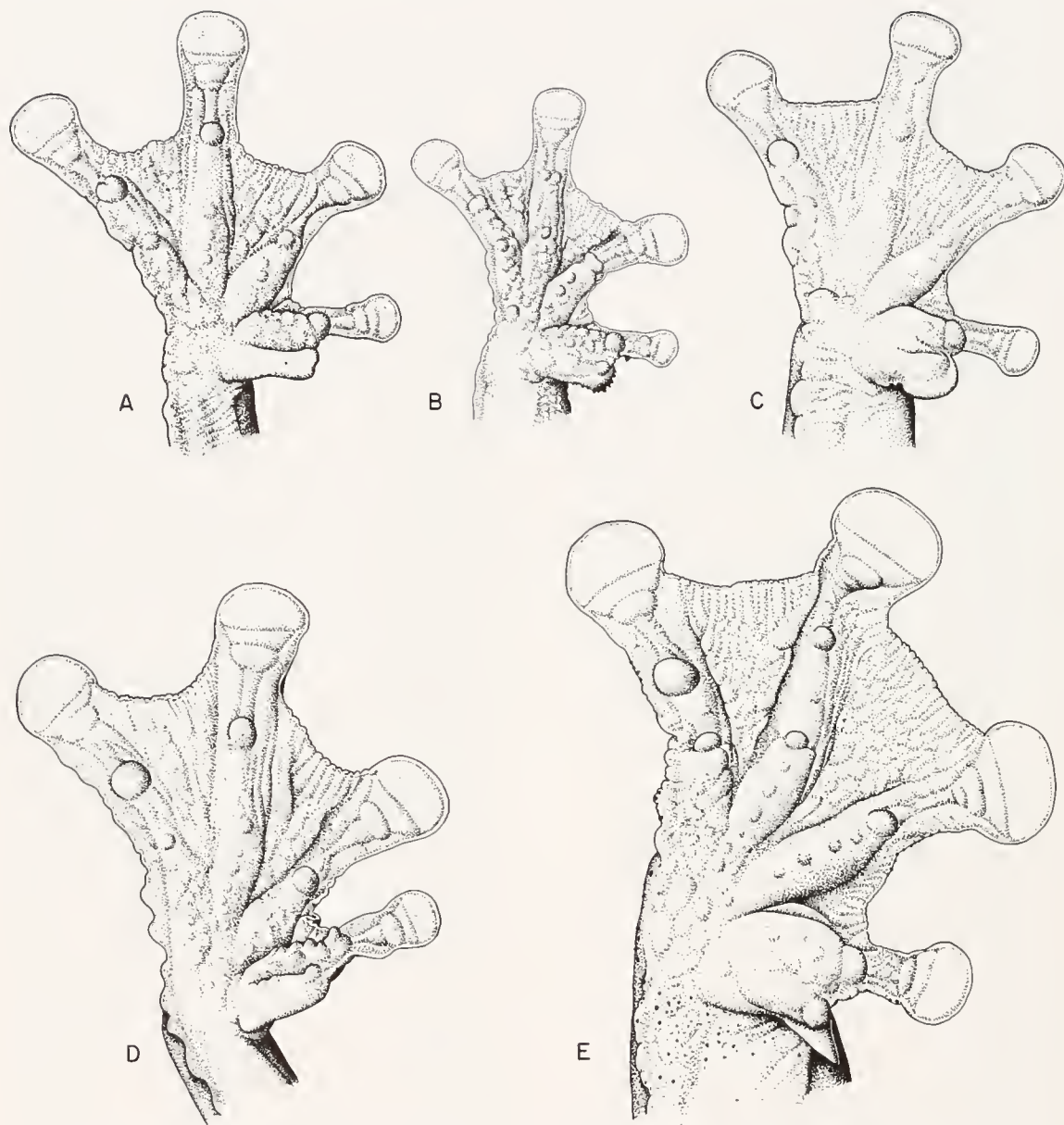


FIG. 166. Hands of the fringe-limbed *Hyla*. A. *H. valancifer*, K.U. No. 95416. B. *H. echinata*, U.I.M.N.H. No. 49339. C. *H. finbrimembra*, R.C.T. No. 761. D. *H. thysanota*, U.S.N.M. 151080. E. *H. miliaria*, K.U. No. 30404. $\times 2$.

***Hyla valancifer* Firschein and Smith**

Hyla valancifer Firschein and Smith, 1956, p. 18 [holotype, U.I.M.N.H. No. 35398 from Volcán San Martín, Veracruz, México; 1. Lester Firschein collector]. Duellman, 1960a, p. 55.

DIAGNOSIS: This large species (82 mm.) has a smooth dorsum, scalloped fringes, and

the fingers about two-thirds webbed; there is no integumentary-cranial co-ossification, and adult males have an ovoid, flattened spade-like, projecting prepollex. The dorsum, flanks, and thighs are reddish brown with dull green markings. *Hyla echinata* differs by being smaller (60 mm.) and by having

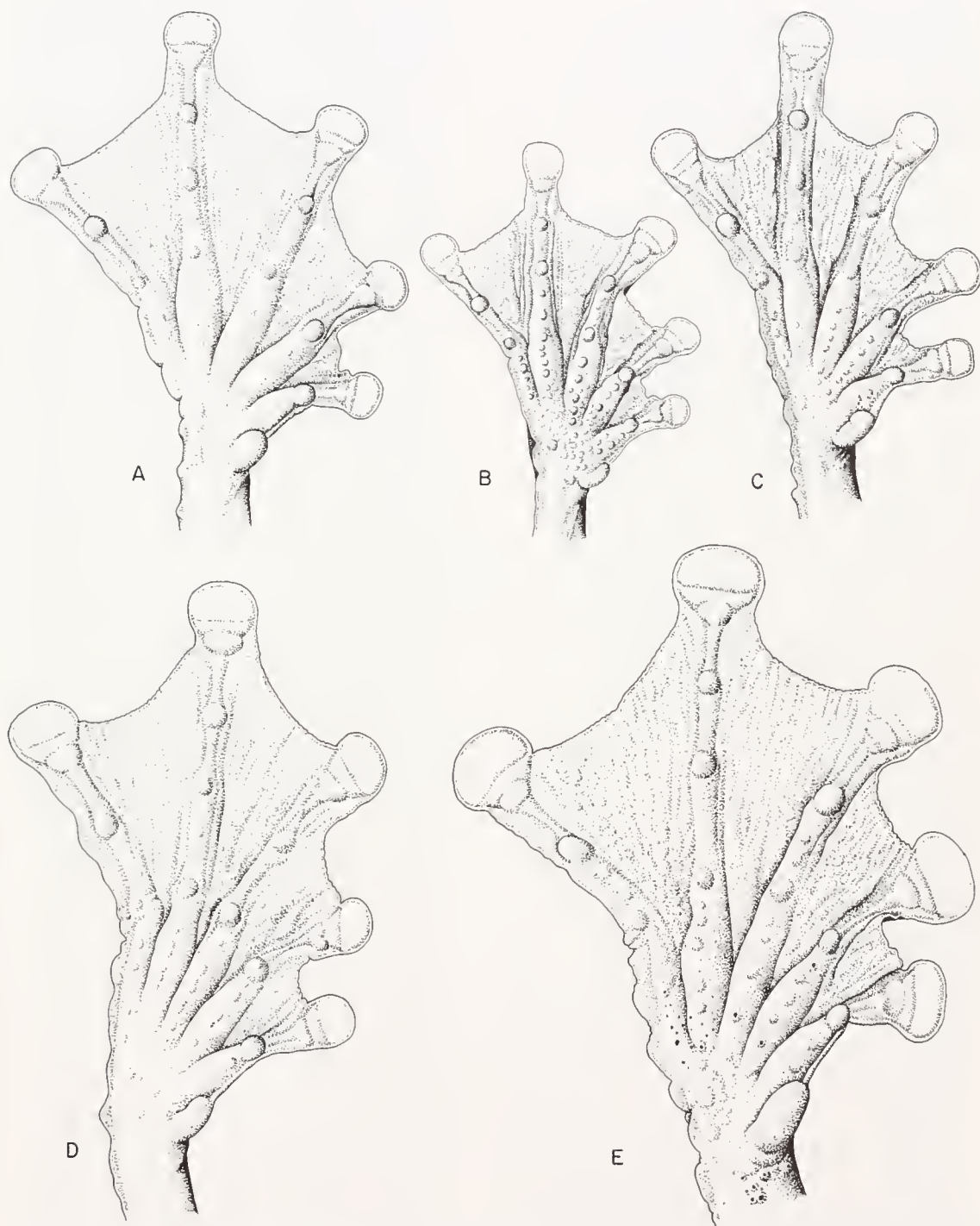


FIG. 167. Feet of the fringe-limbed *Hyla*. A. *H. valancifer*, K.U. No. 95416. B. *H. echinata*, U.I.M.N.H. No. 49339. C. *H. fimbriatimembra*, R.C.T. No. 761. D. *H. thysanota*, U.S.N.M. No. 151080. E. *H. miliaria*, K.U. No. 30404. $\times 2$.

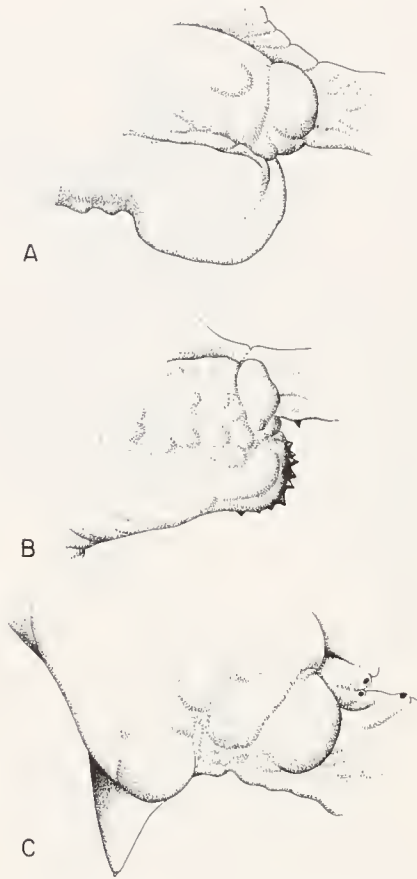


FIG. 168. Palmar view of right prepollices of males of fringe-limbed *Hyla*. A. *H. valancifer*, K.U. No. 95416. B. *H. echinata*, U.I.M.N.H. No. 49339. C. *H. miliaria*, K.U. No. 30404. $\times 5$.

dark brown flanks and anterior and posterior surfaces of the thighs contrasting with a pale reddish brown dorsum; breeding males have a clump of nuptial spines on a blunt prepollex. *Hyla miliaria* has a tuberculate dorsum, fully webbed fingers, and a projecting prepollical spine. *Hyla finbrimembra* has integumentary-cranial co-ossification and a creamy tan dorsum. *Hyla thysanota* has fully webbed hands and feet and a green dorsum.

DESCRIPTION: This is a large species. The one adult male has a snout-vent length of 77.7 mm., and one adult female has a snout-vent length of 82.0 mm. The following proportions are for the male and female respectively. The ratio of tibia length to snout-vent length is 0.489 and 0.501; the ratio of foot length to snout-vent length is 0.459 and 0.432;

the ratio of head length to snout-vent length is 0.318 and 0.317; the ratio of head width to snout-vent length is 0.369 and 0.371, and the ratio of the diameter of the tympanum to that of the eye is 0.831 and 0.782. In two juveniles, having snout-vent lengths of 22.0 and 35.4 mm., the ratio of tibia length to snout-vent length is 0.536 and 0.531, respectively, and the ratio of the diameter of the tympanum to that of the eye is 0.565 and 0.568, respectively. In other proportions, the juveniles do not differ from the adults.

The head is about as wide as the body; the top of the head is flat; and the eyes are moderately large and prominent. In dorsal profile, the head is rounded, but the narial region forms a blunt, slightly indented, snout. In lateral profile, the snout is truncate. The snout is moderately long, and the nostrils are noticeably protuberant and situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is rounded and barely discernible posteriorly, but distinct and slightly elevated anteriorly. The loreal region is concave, and the lips are moderately thick and slightly flared. A moderately heavy supratympanic fold extends from the posterior corner of the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold covers the upper part of the tympanum, which otherwise is distinct and slightly elevated. The tympanum is posteroventral to the eye and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately short and robust. A low, scalloped dermal fold extends from the elbow along the ventrolateral edge of the forearm and fourth finger to the base of the disc; a distinct transverse dermal fold is present on the wrist. Fingers are moderately long and robust and bear large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large, round, and flattened; none is bifid. The supernumerary tubercles are small and present in two rows on the proximal segments of the second, third, and fourth fingers. A large flat palmar tubercle is confluent with the prepollex, which is enlarged and in an adult male bears a flat, oval, spade-like projection (fig. 168A). The fingers are about

two-thirds webbed in adults (fig. 166A). The webbing extends from the base of the penultimate phalanx of the first finger to the distal end of the antepenultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, and on to the base of the disc of the fourth finger. The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. Two or three large tubercles are present on the heel and a low tarsal fold extends the full length of the tarsus. A low, scalloped fringe is present on the ventrolateral edge of the tarsus and fifth toe. The inner metatarsal tubercle is elliptical, flat, and has a raised medial edge. The outer metatarsal tubercle is low, elongate, and rounded. The toes are moderately long and bear discs that are distinctly smaller than those on the fingers. The subarticular tubercles are small and subconical, and the supernumerary tubercles are small and indistinct. The toes are about four-fifths webbed (fig. 167A). The webbing extends from the base of the disc of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the middle of the penultimate phalanx of the third, from the base of the disc of the third to the middle of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the level of the dorsal surfaces of the thighs. A short anal sheath is present, and a few small tubercles are present below the anal opening. In adults, this skin on the dorsum is smooth, except for a few small tubercles in the interorbital area and on the supratympanic fold. In juveniles, the dorsal surfaces of the head, body, and limbs are tuberculate. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; that on the other ventral surfaces is smooth. The tongue is nearly round, shallowly notched behind and barely free posteriorly. The denticulous processes of the prevomers are transverse ridges between the moderately small, round choanae. One adult male has nine teeth on each prevomerine process, and one

adult female has seven and eight prevomerine teeth. A small female (snout-vent length, 35.4 mm.) has a total of 11 prevomerine teeth. The vocal slits extend a short distance posterolaterally from the midlateral base of the tongue. Apparently the vocal sac is single, median, and subgular.

The general coloration of *Hyla valancifer* is a mottled dull green and brown dorsum with orange spots on the flanks (pl. 2, fig. 3). Notes on the color in life of an adult female (U.M.M.Z. No. 122745) provided by Douglas C. Robinson are as follows: "The dorsum is mottled green and brown with some tan; the flanks are marked with orange spots on a pinkish tan ground color. A dark brown streak extends from the eye to the nostril. The posterior surfaces of the thighs and webbing is purplish pink. The fringes are pinkish tan and the chin is a salmon-color. The tympanum is greenish bronze, and the iris is dark brown."

A juvenile female had a pale tan dorsum mottled with dark green; the flanks were mottled with ivory and dark chocolate brown (pl. 57, fig. 5). The posterior surfaces of the thighs were reddish brown mottled with cream, and the webbing was reddish brown. The iris was a metallic reddish brown. Duellman (1960a, p. 57), in describing this juvenile female, noted that when the frog was collected the green on the dorsum was pale and iridescent. During the two weeks that the frog was kept alive, the dorsal ground color often changed to dark reddish brown with olive-green markings, or to pale tan with pale green markings.

In preservative, the adults are dull reddish brown with irregular dark brown markings on the dorsum and dorsal surfaces of the limbs. The flanks are somewhat paler. The throat is pale reddish tan, and the belly is creamy white with a suffusion of brown laterally. The webbing on the hands and feet is dark brown.

TADPOLES: The tadpoles of this species have not been found.

MATING CALL: The mating call of this species is unknown.

NATURAL HISTORY: The four known specimens of *Hyla valancifer* have been collected in cloud forests. I obtained a juvenile female at night. The frog was on the upper side of a

palm frond about 8 meters above the ground in a shallow ravine. Nothing is known about the habits and life history of this species.

REMARKS: Firschein and Smith (1956, p. 18) named *Hyla valancifer* on the basis of a single juvenile having a snout-vent length of 22.0 mm. Duellman (1960a, pp. 55-57) reported a second specimen of this species, a juvenile female having a snout-vent length of 35.4 mm. Due to the energetic efforts of Douglas C. Robinson, two adults of this species are now available. The juveniles differ from the adults in several features. They have proportionately longer legs and smaller tympani, and they have slightly less webbing. Juveniles have a tuberculate dorsum, whereas in adults the skin on the dorsum is smooth except for a few small, low tubercles on the head. The snout in juveniles is more truncate than in adults.

Were it not for the fact that the two juveniles and the two adults were all collected on the same isolated mountain, it might be supposed that the juveniles represent a species distinct from the adults. Despite the obvious differences, the similarities overwhelmingly suggest that the two small specimens are merely juveniles of this large species.

ETYMOLOGY: The specific name *valancifer*, is derived from the English valance and the Latin suffix *-fer* meaning to have and is used in the sense of the frog having a decorative valance-like fringe on the limbs.

DISTRIBUTION: *Hyla valancifer* is known only from elevations of about 1200 meters on Volcán San Martín, in the Sierra de los Tuxtlas, in southern Veracruz, México (fig. 169).

See Appendix 1 for the locality records of the four specimens examined.

Hyla echinata Duellman

Hyla echinata Duellman, 1962, p. 349 [holotype, U.I.M.N.H. No. 49339 from Campamento Vista Hermosa, Oaxaca, México; O. C. Van Hyning collector].

DIAGNOSIS: This species lacks cranial-integumentary co-ossification and osteoderms; it has a smooth dorsum, the fingers about two-thirds webbed, and a cluster of horny spines on a projecting prepollex in males. The flanks and anterior and posterior surfaces of the thighs are dark brown and sharply demarked from the pale reddish brown dorsum. *Hyla*

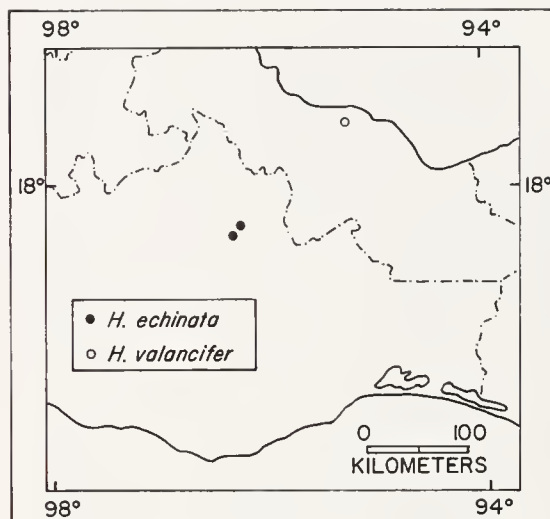


FIG. 169. Distribution of *Hyla valancifer* and *echinata*.

valancifer differs from *echinata* by being much larger and by having the flanks and dorsum reddish brown; in males of *valancifer* the prepollex bears a smooth spade-like projection. *Hyla miliaria* differs from *echinata* by having nearly fully webbed hands and a tuberculate dorsum, and *fimbrimembra* differs by having cranial-integumentary co-ossification and creamy tan dorsum, flanks, and thighs. The only other Middle American fringe-limbed hyliid is *Hyla thysanota*, which is much larger (95 mm.) than *echinata* and has a green dorsum and scalloped fringes.

DESCRIPTION: This is a moderately large species known only from two specimens. The snout-vent length of an adult male is 57.0 mm. and of an adult female, 60.2 mm. In the male and female, respectively, the ratio of tibia length to snout-vent length is 0.535 and 0.500; the ratio of foot length to snout-vent length is 0.465 in each; the ratio of head length to snout-vent length is 0.347 and 0.357; the ratio of head width to snout-vent length is 0.308 and 0.312, and the ratio of the diameter of the tympanum to that of the eye is 0.768 and 0.774.

The head is wider than the body; the top of the head is flat, and the eyes are moderately large and prominent. In dorsal profile, the lips form a broadly rounded snout, but the internarial area is truncate; in lateral profile, the snout is truncate. The snout is moderately

long; the nostrils are barely protuberant and situated at a point about five-sixths of the distance from the eyes to the tip of the snout. The canthus is rounded and moderately elevated; the loreal region is concave and the lips are moderately thick and slightly flared. A dermal fold extends posteriorly from the orbit, above the tympanum, and downward to a point above the insertion of the arm. The upper edge of the tympanum is obscured by the dermal fold; otherwise, the tympanum is distinct and elevated above the surrounding skin. The tympanum is posteroventral to the eye and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately short and robust. A thin, shallowly scalloped dermal fold extends from the elbow along the ventrolateral edge of the forearm and fourth finger to the base of the disc on the fourth toe. A distinct transverse dermal fold is present on the wrist. The fingers are moderately long and bear large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and subconical; the terminal tubercle on the third and fourth fingers of the right hand in the male are slightly bifid. The supernumerary tubercles are small and conical; they are numerous on the proximal segments of all digits. The prepollex is greatly enlarged; an elongate, triangular tubercle is present; the distal end of the prepollex bears a clump of horny spines in the adult male (fig. 168B). The fingers are about two-thirds webbed (fig. 166B). The webbing extends from the base of the penultimate phalanx of the first finger to the distal end of the antepenultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the penultimate phalanx of the third and on to the middle of the penultimate phalanx of the fourth finger. The legs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth the length of the shank. The tibiotarsal articulation extends to the nostril. A few small tubercles are present on the heel, and a low, thin, tubercular tarsal fold extends from the heel along the ventrolateral edge of the tarsus and fifth toe to the base of the disc. The inner

metatarsal tubercle is moderately small, elliptical, flat, and broadly visible from above. The outer metatarsal tubercle is absent. The toes are moderately short and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are small and subconical; the supernumerary tubercles are small, conical, and numerous on the proximal segments of all digits. The toes are nearly fully webbed (fig. 167B). The webbing extends from the base of the disc of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the middle of the penultimate phalanx and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the level of the upper surfaces of the thighs. A short anal sheath and a few tubercles below the anus are present. The skin on the throat, belly and ventral surfaces of the arms and thighs is granular; that on the ventral surfaces of the tarsi is finely granular, and the skin on the dorsum and ventral surface of the shank is smooth. The tongue is broadly cordiform, shallowly notched behind, and barely free posteriorly. The denticulous processes of the prevomers are narrowly separated transverse ridges between small, round choanae. In each specimen, there are seven teeth on each process, for a total of 14 prevomerine teeth in each specimen. The vocal slits are short and extend posterolaterally for a short distance from the midlateral base of the tongue. The vocal sac is single, median, and subgular.

The general coloration of *Hyla echinata* is pale reddish brown above with dark brown flanks (pl. 2, fig. 2). Notes on the coloration in life of an adult female were provided by Dale L. Hoyt. He described the dorsum as being pale reddish brown; the flanks and anterior surfaces of the thighs are dark brown, and this lateral color is clearly demarked from the paler dorsal color. The posterior surfaces of the thighs are dark brown, almost black. The ventral surfaces of the shanks and feet, and the webbing, is dark brown. A few creamy yellow flecks are present on the flanks, and a transverse white line is present above

the anus. The belly is dusty cream, and the tympanum is coppery tan.

In preservative, the dorsum is dull reddish tan or purplish brown. The flanks, anterior and posterior surfaces of the thighs, and the webbing on the hands and feet are purplish black. The venter is dull creamy tan, except on the shanks and feet, which is brown. A faint suffusion of brown is noticeable on the chin. There is a narrow creamy tan line along the margin of the upper lip and a creamy white stripe above the anus. The fringes on the feet and forearms are creamy tan, and the tympanum is coppery tan.

TADPOLES: The tadpoles of this species have not been found.

MATING CALL: The mating call of this species is unknown.

NATURAL HISTORY: *Hyla echinata* is known only from the cloud forest in the mountains of northern Oaxaca, México. One specimen was obtained from a bromeliad, and the other was found on a branch of a tree near a stream in the cloud forest.

REMARKS: *Hyla echinata* seems to be most closely related to *Hyla valancifer*, from which it differs principally by having emarginate, instead of scalloped, fringes and spiny nuptial excrescences, instead of a spade-like prepolex. Insofar as known, *echinata* is the only fringe-limbed hylid having nuptial excrescences composed of a cluster of horny spines.

ETYMOLOGY: The specific name is Latin and means spiny or thorny and is used in reference to the nuptial excrescences in the breeding male.

DISTRIBUTION: *Hyla echinata* is known only from cloud forests at elevations of about 1500 meters on the northern slopes of the Sierra de Juarez in northern Oaxaca, México (fig. 169).

See Appendix 1 for the locality records of the two specimens examined.

Hyla fimbrimembra Taylor

Hyla richardi Taylor 1948b, p. 233 [holotype, R.C.T. No. 761 from the American Cinchona Plantation, Alajuela Province, Costa Rica; Richard C. Taylor collector (not *Hyla richardii* Baird, 1854 (= *Hyla versicolor*) from Cambridge, Massachusetts)]; 1952c, p. 819.

Hyla fimbrimembra Taylor, 1948b, p. 235 [holotype, R.C.T. No. 764 from Isla Bonita, Heredia Prov-

ince, Costa Rica; Richard C. Taylor collector]; 1952c, p. 821.

Hyla richarditaylori Taylor 1954b, p. 624 [replacement name for *Hyla richardi* Taylor, 1948, preoccupied].

DIAGNOSIS: In adults of this species the skin is co-ossified with the underlying cranial elements on the top of the skull; the dorsum is minutely granular (tubercular in juveniles), and the hands are about two-thirds webbed. The dorsum, flanks, and limbs are creamy tan; faint, darker, narrow bands are present on the limbs. *Hyla fimbrimembra* differs from all other known fringe-limbed hylids by having integumentary-cranial co-ossification and from all other Middle American hylids with co-ossified skulls by having dermal fringes on the outer edges of the limbs.

DESCRIPTION: This species is represented in collections by one juvenile and one adult female having a snout-vent length of 70.8 mm. In the latter specimen, the ratio of tibia length to snout-vent length is 0.517; the ratio of foot length to snout-vent length is 0.465; the ratio of head length to snout-vent length is 0.350; the ratio of head width to snout-vent length is 0.372, and the ratio of the diameter of the tympanum to that of the eye is 0.780. The juvenile has a snout-vent length of 29.7 mm.; the proportions of the limbs and head are larger than in the adult, and the tympanum is proportionately smaller (tympanum/eye ratio, 0.595).

The head is slightly wider than the body; the top of the head is flat, and the eyes are prominent. The skin on the top of the head posterior to the anterior edges of the orbit is co-ossified with the underlying cranial elements. In dorsal profile, the snout is acutely rounded; in lateral profile, the snout slopes abruptly from the nostrils to the edge of the upper lip. The snout is moderately long; the nostrils are protuberant and situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is rounded, but not elevated; the loreal region is concave, and the lips are moderately thin and somewhat flared. A thin dermal fold extends posteriorly from the orbit, above the tympanum, and downward towards the angles of the jaws; at a point about midway between the upper edge of the tympanum and the angles of the jaws, the fold curves posteriorly and

terminates at a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and elevated; the tympanum is separated from the eyes by a distance equal to about one and one-half times the diameter of the tympanum.

The arms are moderately long and slender. A thin transverse dermal fold is present on the wrist, and a broad, sharply scalloped dermal fringe extends the length of the forearm from the elbow to the base of the disc of the fourth finger. The fingers are moderately long and robust and bear large discs. The disc on the third finger is slightly larger than the tympanum. The subarticular tubercles are moderately large and conical; none are bifid. The supernumerary tubercles are conical and present in a single row on the proximal segments of each digit except that additional tubercles are present on the thumb and on the base of the fourth finger. The palmar tubercle is small and conical. The prepollex is elongate, rectangular, and blunt terminally. The fingers are about two-thirds webbed (fig. 166C). The webbing is vestigial between the first and second fingers, and extends from the base of the disc of the second to the distal end of the antepenultimate phalanx of the third and from the base of the penultimate phalanx of the third to the base of the disc of the fourth finger. The legs are long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A thin transverse dermal fold and several pointed tubercles are present on the heel. A thin, sharply scalloped dermal fringe is present on the outer edge of the tarsus from the heel to the base of the disc of the fifth toe. A fringe-like, elevated tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is elongate, flattened, and barely visible from above. The outer metatarsal tubercle is small and conical. The toes are moderately long and slender, and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are small and round. The supernumerary tubercles are very small and subconical; they are irregularly arranged in a single row on the proximal segment of each digit. The toes are about three-fourths webbed (fig. 167C). The webbing extends from the

distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the base of the disc of the second to the base of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate phalanx of the fourth, and on to the base of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs. A short anal flap is present; and there are granular dermal folds extending ventrolaterally from the anal opening. The dorsal surfaces are smooth, except for small tubercles on the dorsal surfaces of the limbs. The skin on the throat, belly, and ventral surfaces of the thighs is granular, and that on the other ventral surfaces is smooth. The tongue is cordiform, shallowly notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are narrowly separated transverse ridges between the moderately large, round choanae. Eight teeth are present on each process.

Structurally, the juvenile differs from the adult female just described by having a more truncate snout in dorsal profile and a definitely truncate snout in lateral profile. The dermal folds below the anal opening are more prominent in the juvenile. Small tubercles are present on the dorsal surfaces of the head and body, as well as on the limbs, in the juvenile. The juvenile specimen lacks integumentary-cranial co-ossification.

According to Taylor (1948b, p. 234) the color in life of the adult female (R.C.T. No. 761) was "nearly uniform lavender brown with very indistinct darker markings; discs on all fingers and toes blue-black; edge of lower jaw bluish black; a narrow line of black on edge of upper lip; throat yellow-brown with fine purple reticulations; venter and underside of thighs lavender brown with cream marks; underside of hands and feet lavender; no light mark on vent." Taylor (1948b, p. 237) described the color of the juvenile (R.C.T. No. 764) as follows: "Brownish gray above, the extremities more ashen gray; chin and venter white with strong lavender reticulations on skin; on edge of underside of arms is deep lavender stripe; elevated area on head blackish brown; limbs very faintly barred; some

brown flecks forming a short diagonal line on thighs; some flecks of brown in groin."

In preservative, the dorsum of the adults is pale tan with a few small purplish brown spots on the back and faint, narrow brown bars on the limbs (pl. 3, fig. 1). The venter is creamy tan. The edge of the upper lip, the edge of the chin, and the discs on the fingers and toes are lavender-brown. The juvenile is colored like the adult, except that the bands on the limbs are more prominent, and small dark flecks are present on the flanks. The juvenile lacks the dark color on the discs and on the edges of the upper lip and chin, whereas it possesses fine dark brown reticulations on the chin.

TADPOLES: The tadpoles of this species have not been found.

MATING CALL: The mating call of this species is unknown.

NATURAL HISTORY: The two specimens of *Hyla fimbrimembra* were obtained in humid montane forests. The juvenile was found clinging to a small plant bathed in the spray of a waterfall at night (Taylor, 1952c, p. 824). The adult was found by day beneath the bark of a standing dead tree (Taylor, personal communication).

REMARKS: Taylor (1948b) named two species of fringe-limbed tree frogs from Costa Rica—*Hyla richardi* and *Hyla fimbrimembra*. *Hyla richardi* Taylor, 1948b, is preoccupied by *Hyla richardii* Baird, 1854; this was noted by Taylor (1954b), who proposed the replacement name, *Hyla richardtaylori* for *Hyla richardi* Taylor, 1948b. I am treating *Hyla richardtaylori* and *Hyla fimbrimembra* as conspecific. Although *Hyla richardi* Taylor has page priority over *Hyla fimbrimembra* Taylor, because the former is preoccupied and was given the replacement name *Hyla richardtaylori* in 1954, the correct name for this frog is now *Hyla fimbrimembra*.

There is little doubt but what the two specimens on which Taylor (1948b) based his descriptions of two species represent a single taxon. Although one specimen is a juvenile, it is like the adult, and differs from all other known fringe-limbed hylids, by having the curved supratympanic fold, dermal folds below the anal opening, sharply scalloped fringes on the arms and feet, and narrow dark trans-

verse bands on the limbs. The juvenile differs from the adult by lacking integumentary-cranial co-ossification and by having a more blunt snout and tuberculate dorsum. The ontogenetic change in the shape of the snout and in the tuberosity parallels the change in the closely related *Hyla valancifer*. The absence of co-ossification apparently is characteristic of juveniles of species in which the skin becomes co-ossified with the underlying cranial elements in the adult (Trueb, 1966 and 1969).

ETYMOLOGY: The specific name is derived from the Latin *fimbria*, meaning fringe, and the Latin *membrum*, meaning part of member and refers to the dermal fringes on the limbs.

DISTRIBUTION: *Hyla fimbrimembra* is known only from elevations of about 1500 meters on the Caribbean slopes of Volcán Poás in Costa Rica (fig. 170).

See Appendix 1 for the locality records of the two specimens examined.

Hyla thysanota Duellman

Hyla thysanota Duellman, 1966a, p. 259 [holotype, U.S.N.M. No. 151080 from Cerro Malí, Darién Province, Panamá, elevation 1265 meters; Charles O. Handley, Jr. collector].

DIAGNOSIS: This large (95 mm.) species differs from all other known fringe-limbed hylids by having a uniformly green dorsum. The skin on the dorsum is granular, and the hands and feet are fully webbed; there is no integumentary-cranial co-ossification. All other moderate to large green hylids in Middle America lack scalloped dermal fringes on the outer edges of the limbs.

DESCRIPTION: This large species is known from a single female having a snout-vent length of 95.7 mm. The ratio of tibia length to snout-vent length is 0.533; the ratio of foot length to snout-vent length is 0.466; the ratio of head length to snout-vent length is 0.325; the ratio of head width to snout-vent length is 0.381; and the ratio of the diameter of the tympanum to that of the eye is 0.578.

The head is wider than the body, and the top of the head is flat. In dorsal profile, the snout is broadly rounded, and in lateral profile, it is round. The snout is moderately long; the nostrils are protuberant laterally and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The

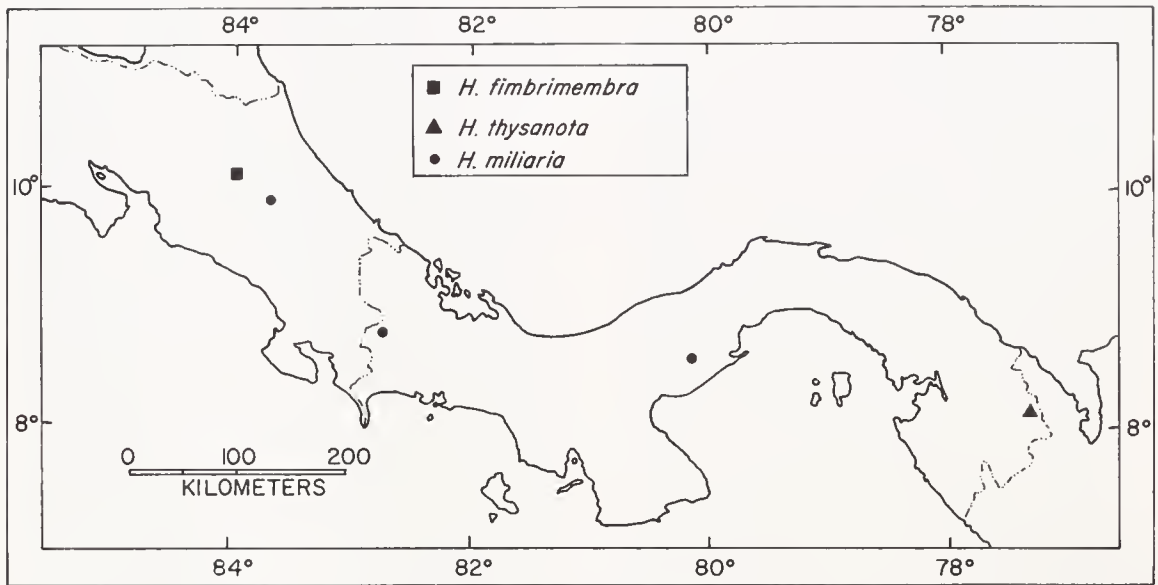


FIG. 170. Distribution of *Hyla miliaria*, *thysanota*, and *fimbriemembra*.

canthus is heavy and rounded; the loreal region is deeply concave, and the lips are broad and flaring. A moderately heavy dermal fold extends posteriorly from the eye to the point above the insertion of the arm. The upper edge of the tympanum is obscured by the dermal fold; otherwise, the tympanum is distinct.

The arms are moderately long and slender. Two thin transverse dermal folds are present on the wrist, and a thin, scalloped dermal fringe extends along the outer edge of the forearm from the elbow to the disc of the fourth finger. The fingers are moderately short and robust and bear large discs; the discs on all fingers, except the first, are larger than the tympanum. The distal subarticular tubercle on the fourth finger is flattened; the other subarticular tubercles are large and conical. The supernumerary tubercles are small, conical, and numerous on the proximal segments of each digit. There is no palmar tubercle, but an elongate, flat tubercle is present on the prepollex, which is only moderately enlarged. The fingers are nearly fully webbed (fig. 166D). The webbing extends to the bases of the penultimate phalanges between the first and second fingers and connects the other fingers at the bases of the discs. The legs are moderately long and slender; the heels of the

adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the eye. A distinct transverse dermal fold is present on the heel, and a thin tarsal fold curves from the heel to the inner metatarsal tubercle. A thin, scalloped dermal fringe extends along the outer edge of the foot from the heel to the disc of the fifth toe. The inner metatarsal tubercle is flat, broadly elliptical and visible from above; the outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are conical; the supernumerary tubercles are small, conical, and in a single row on the proximal segment of each digit. The toes are fully webbed (fig. 167D).

The anal opening is directed posteriorly at the midlevel of the thighs. The anal sheath is short and granular; a distinct granular dermal fold is present on each side of the anal opening. The skin on the top of the head and body is finely granular; that on the belly and median posteroventral surfaces of the thighs is granular, whereas that on the other surfaces is smooth. The tongue is broadly cordiform, shallowly notched posteriorly, and barely free behind. The dentigerous processes are narrowly separated transverse ridges between the

small, round choanae. There are 10 teeth on one ridge and 11 on the other.

According to color notes taken by Charles O. Handley, Jr., in life the dorsum was green, and the ventral surfaces were pinkish white; the iris was brown. In preservative, the dorsum was dark purplish brown (pl. 3, fig. 2). The lower parts of the flanks, the anterior and posterior surfaces of the thighs, and the ventral surfaces of the hind limbs are pale brown; the webs are dark brown. The belly is creamy yellow with brown spots anteriorly, and the chin is brown. The upper lip is gray-white.

TADPOLES: The tadpoles of this species have not been found.

MATING CALL: The mating call of this species is unknown.

NATURAL HISTORY: The only known specimen was found in a tree top at night in humid montane forest near the head waters of the Río Pucro.

REMARKS: Nothing can be added to the original description by Duellman (1966a).

ETYMOLOGY: The specific name is derived from the Greek *thysanotos*, meaning fringed, and refers to the dermal fringes on the arms and feet.

DISTRIBUTION: *Hyla thysanota* is known from an elevation of 1265 meters on the east slope of Cerro Malí in the Serranía del Darién in eastern Panamá (fig. 170).

See Appendix 1 for the locality record of the one specimen examined.

Hyla miliaria (Cope)

Hypsiboas miliaris Cope, 1886, p. 272 [holotype, U.S.N.M. No. 14193 from "Nicaragua"; John F. Bransford collector].

Hyla miliaria: Günther, 1901 (1885-1902), p. 283.

Hyla phantasmagoria Dunn, 1943, p. 309 [holotype, M.d.L.S. No. 267 from the Río Cauca, Antioquia-Bolívar border, Colombia; Hermano Daniel collector].

Plectrohyla miliaria: Taylor and Smith, 1945, p. 596.

Hyla immensa Taylor, 1952c, p. 815 [holotype, K.U. No. 30404 from the Instituto Interamericano de Ciencias Agrícolas, 2 kilometers east of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor collector].

DIAGNOSIS: This huge frog (106 mm.) is readily distinguished from all other Middle American hylids by having a tuberculate dorsum in juveniles and adults, fully webbed

hands and feet, and in adults osteoderms, which give the head the appearance of having the skin co-ossified with the underlying cranial elements. The tips of the granules on the venter are keratinized in adults, and in breeding males the prepollical spine is protruding. Superficially, *Hyla miliaria* resembles the West Indian *Hyla lichenata* in size and the tuberculate dorsum, but the latter is casque-headed.

DESCRIPTION: This is the largest known species of fringe-limbed hylids. Four males have snout-vent lengths of 57.2 to 106.0 mm.; the ratio of tibia length to snout-vent length is 0.466 to 0.566 (mean, 0.525); the ratio of foot length to snout-vent length is 0.420 to 0.533 (mean, 0.471); the ratio of head length to snout-vent length is 0.317 to 0.365 (mean, 0.340); the ratio of head width to snout-vent length is 0.360 to 0.410 (mean, 0.386), and the ratio of the diameter of the tympanum to that of the eye is 0.493 to 0.753 (mean, 0.642). The single known female has a snout-vent length of 69.7 mm. and in proportions does not exceed the limits of variation known in the males. One juvenile has a snout-vent length of 41.3 mm.

The head is as wide as the body and the top of the head is flat. In dorsal profile, the head is rounded, and the snout is truncate; in lateral profile the snout is truncate. The snout is short, and the nostrils are protuberant and situated at a point about five-sixths of the distance from the eyes to the tip of the snout. The internarial area is noticeably depressed. The canthus is rounded, and the loreal region is deeply concave; the lips are moderately thick and flared. A bony ridge followed by a dermal fold extends posteriorly from the eye above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct, elevated, and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are short and extremely robust. A heavy transverse dermal fold is present on the wrist. A heavy, scalloped dermal fringe extends along the ventrolateral edge of the forearm from the elbow to the wrist and then along the outer edge of the fourth finger. The hand is immense. The fingers are moderately long and robust and bear huge discs;

the width of the disc on the third finger is half again as wide as the diameter of the tympanum. The subarticular tubercles are large; the distal one on the fourth finger is flattened and in some specimens, it is bifid; the other subarticular tubercles are round. The supernumerary tubercles are large, conical, and arranged in a single row on the proximal segment of each digit. A flat, partially bifid palmar tubercle is present. The prepollex is greatly enlarged and curved backwards terminally. In one large male the prepollical spine protrudes from the prepollex (fig. 168C). The fingers are nearly fully webbed (fig. 166E). The webbing extends from the base of the penultimate phalanx of the first finger to the base of the penultimate phalanx of the second and connects the other fingers at the bases of the webs. The legs are moderately long and robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A distinct, transverse dermal fold is absent on the heel, but numerous small tubercles are present on the heel. A broad, thin, scalloped dermal fringe extends from the heel along the ventrolateral edge of the tarsus to the base of the disc on the fifth toe. A distinct, curved, tarsal fold is present. The inner metatarsal tubercle is elongately elliptical with an elevated outer edge. Several small tubercles are present distally on the tarsus, so it is impossible to determine if an outer metatarsal tubercle, *per se*, is present. The toes are moderately long and robust and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are large and subconical, and the supernumerary tubercles are small, conical, and arranged in a single row on the proximal segments of each digit. The toes are webbed to the bases of the discs (fig. 167E).

The anal opening is directed posteroventrally at the midlevel of the thighs. A broad, granular anal sheath is present, and many pointed tubercles are present below the anal opening. The skin on the dorsum is tubercular. Tubercles are best developed on the head and midthoracic region. Apparently, in large individuals, osteoderms are present in the skin, and possibly there is a small amount of integumentary-cranial co-ossification; in the

two largest specimens, the skin seems to be co-ossified with the skull, but in an adult male having a snout-vent length of 70.2 mm. the skin is not co-ossified with the underlying cranial elements. The skin on the throat, belly, and ventral surfaces of the arms and thighs is granular. In the two largest specimens (both having snout-vent lengths of more than 100 mm.) the tubercles have horny tips. The ventral surfaces of the shanks are smooth. The tongue is broadly cordiform, barely free behind, and only shallowly, if notched at all, posteriorly. The dentigerous processes of the prevomers are elongate, narrowly separated, transverse ridges between the posterior margins of the moderately large, ovoid, choanae. Four males have nine to 17 teeth on each process and a total of 19 to 33 (mean, 23.8) prevomerine teeth; the one female has nine teeth on one process and 11 on the other. The vocal slits extend from the posterolateral base of the tongue towards the angles of the jaws. The vocal sac is single, median, and subgular.

The general coloration of *Hyla miliaria* is mottled brown and tan (pl. 44, fig. 1). The coloration in life of an adult male (K.U. No. 101610) was as follows: the dorsum was mottled dark brown, orange-tan, and metallic green. The chin was pale brown with dark brown spots and white tubercles. The belly was pale tan, and the ventral surfaces of the legs were pinkish tan. The anterior and posterior surfaces of the thighs were pale brown with dark brown mottling. The webbing and the discs were brown with dark brown streaks on the former and flecks on the latter. The anal region was creamy white, and the tympanum was brown. The iris was bronze with reddish brown reticulations, and the palpebrum was pale tan mottled with dark metallic green.

In preservative, the four males and one juvenile are dull brown with darker brown markings, consisting of irregular bronze reticulations on the back and faint transverse bands on the limbs. The venter in the two largest males is brown mottled with cream, whereas the smaller specimens have a venter that is predominately cream with brown spots. The one female (K.U. No. 98451) is pale tan dorsally with a dark brown inter-

orbital spot and dark brown spots in the sacral region; dark brown transverse bands are present on the limbs, and the venter is immaculate creamy tan, except for small brown flecks on the edge of the chin.

TADPOLES: The tadpoles of this species have not been found.

MATING CALL: Recordings of the call of this species are not available, nor have I heard this species call. Mr. Ratibor Hartmann of Finca Santa Clara, Chiriquí Province, Panamá, told me of hearing a loud growl-like call from a large oak tree in a *cafetal*. We obtained one specimen of *Hyla miliaria* from this oak tree.

NATURAL HISTORY: On the basis of the locality records of *Hyla miliaria*, it is presumed that the species inhabits humid tropical and montane forests. Taylor (1952c, p. 818) obtained one specimen "from mud at the bottom of a water-filled cavity in a tree, about 5 feet above the ground" at Turrialba, Cartago Province, Costa Rica. One specimen from Finca Santa Clara, Chiriquí Province, Panamá, was found at night about 4 meters above the ground on a limb of a tree.

Mr. Louie Hartmann of Finca Santa Clara told me of having seen a large "flying frog" in the forest at Finca Santa Clara. After collecting a specimen of *Hyla miliaria* there, observations were made on the jumping ability of the frog. The frog when leaping, extends the forefeet and the hindlimbs and widely spreads the fingers and toes. The extensive webbing on the large hands and feet, together with the dermal fringes on the arms and feet provide a large surface area. Furthermore, when leaping, the fingers are turned slightly upward (pl. 6). In such a position, the frog is capable of gliding, and this one individual was observed to glide for a distance of about 3 meters while losing less than 1 meter of altitude.

Dunn (1943, p. 311) suggested that the large size, rugosity, big discs, and webbing of *Hyla phantasmagoria* and other fringe-limbed tree frogs were "characters adapting frogs to live in the roof of the forest, under conditions of high evaporation rate. In order to cope with the aridity of the environment, they must become large and rugose, like toads. The great discs are obviously correlated with

the size of frogs and the climbing ability." The rugosity, thickness of the skin, and presence of osteoderms probably do protect the frog from desiccation; the presence of the large discs and the gliding ability indicate that the frogs of this species are strictly arboreal. Probably they do inhabit the forest canopy; consequently, they are rare in collections.

REMARKS: I have compared the holotype of *Hyla phantasmagoria* Dunn, 1943 (M.d.L.S. No. 267) with that of *Hyla immensa* Taylor, 1952c. (K.U. No. 30404), and I have compared the latter with the holotype of *Hyla miliaria* Cope, 1886 (U.S.N.M. No. 14193). Dunn (1943, p. 309) stated that the skin of the head was co-ossified with the skull to form a casque in the type of *Hyla phantasmagoria*. In that specimen, there is partial co-ossification that is the same as in the type of *Hyla immensa*. In the smaller specimens, including the type of *Hyla miliaria*, the skin is not co-ossified with the underlying cranial elements. The only observable difference is structure between the types of *Hyla phantasmagoria* and *Hyla immensa* is that the prepollical spine protrudes in *immensa* and does not in *phantasmagoria*. The spine is not protruding in any of the smaller specimens, including the type of *miliaria*. The nature of the prepollical spine probably is correlated with age and breeding condition. There are differences in proportions among the type specimens, but two individuals from Panamá have proportions that indicate that the differences observed in the types are individual variations within one species.

The amount of dark pigment on the venter is greatest in the largest specimens, the types of *Hyla immensa* and *phantasmagoria*. The type specimen of *Hyla miliaria* has the most contrasting ventral coloration; in this specimen, the venter is cream with large brown spots.

ETYMOLOGY: The specific name is Latin and was used by Cope apparently in the sense of *miliary*, an inflammatory disorder of the skin resulting in the formation of small eruptions—in reference to the tubercular skin.

DISTRIBUTION: *Hyla miliaria* is known definitely from elevations of 600 to 1200 meters on the Caribbean and Pacific slopes of the Costa Rican and western Panamanian highlands and from an unknown locality in Nica-

ragua and from central Colombia (fig. 170).

See Appendix 1 for the locality records of the five specimens examined.

The *Hyla godmani* Group

DEFINITION: The members of this group are medium-sized frogs; males attain a maximum snout-vent length of 45 mm. The dorsum is pale gray or tan to brown. The hidden surfaces of the legs and the webbing is yellow or red. The palpebral membrane is clear. The fingers are about three-fifths webbed and the toes are more than three-fourths webbed. Dermal folds and appendages are lacking on the limbs. An extensive axillary membrane is present. Males have a single, median, subgular vocal sac, but lack horny nuptial excrescences on the pollices. The cranial elements are only moderately ossified (fig. 171), especially with respect to the sphenethmoid, frontoparietals, and otic region. The nasals are small and widely separated medially; the maxillary process of the nasal does not articulate with the maxillary or the palatine. The frontoparietals have a minimal amount of ossification laterally; the large frontoparietal fontanelle is bordered posteriorly by the exoccipitals. The distal one-third of the crista

parotica is cartilaginous; thus the squamosal does not articulate with the bony prootic. The anterior arm of the squamosal extends no more than half of the distance to the maxillary. The well-developed quadratojugal is in bony contact with the maxillary. The pterygoid is robust; the medial ramus articulates with the poorly ossified prootic. Prevomerine teeth are present. The tadpoles are pelagic pond types with moderately deep, terminally pointed caudal fins and anteroventral mouths having two upper and three lower rows of teeth. The mating call consists of a series of loud, quickly repeated notes that have distinct pulses and harmonics. The haploid number of chromosomes is 12 (known only in *loquax*).

COMPOSITION: Two species, *godmani* and *loquax* comprise the group, which is restricted to Middle America. Of these two species, 896 preserved frogs, 20 skeletons, three lots of tadpoles, and two preserved clutches of eggs have been examined.

COMMENTS: Smith and Taylor (1948, p. 79) recognized a "*loquax* group," in which they placed eight species of *Hyla*: *loquax*, *rickardsi* (= *godmani*, *fide* Duellman, 1964c), *rozellae* (= *Ptychohyla e. euthysanota*, *fide* Duellman, 1963c), *picta*, *smithii*, *embraccata*, *robertmertensi*, and *underwoodi* (= *microcephala underwoodi*, *fide* Smith, 1951). The latter two species are members of the *microcephala* group, and *embraccata* is in the *leucophyllata* group. Both of these groups differ osteologically from the *godmani* group by lacking a quadratojugal. Members of these groups have a haploid chromosome number of 15, and their tadpoles have terminal mouths lacking teeth. *Hyla picta* and *smithii* comprise a group differing from the *godmani* group by small size, absence of an axillary membrane, and a mating call consisting of a series of short, high-pitched notes.

The two species in the *godmani* group inhabit humid forested lowlands and foothills. Apparently they differentiated through isolation by the development of subhumid environments in the Isthmus of Tehuantepec in the Pleistocene. At the present time their ranges are narrowly separated, but if they occurred sympatrically the distinctly different mating calls probably would serve as an effective isolating mechanism.

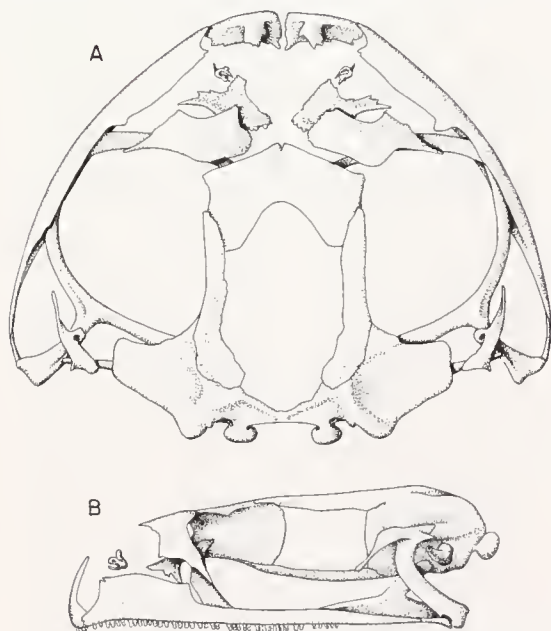


FIG. 171. Dorsal (A) and lateral (B) views of the skull of *Hyla loquax*, K.U. No. 59906. $\times 2.75$.

Hyla godmani Günther

Hyla godmani Günther, 1901 (1885-1902), p. 275 [syntypes, B.M.N.H. Nos. 1901.12.19.88-95 from Jalapa, Veracruz, México; Frederick D. Godman collector; B.M.N.H. No. 1901.12.19.96 from Misanthla, Veracruz, México; Frederick D. Godman collector]. Duellman, 1964c, p. 455 [selection of B.M.N.H. No. 1901.12.19.96 as lectotype].

Hyla miotypanum: Kellogg, 1932, p. 170. Smith and Taylor, 1948, p. 90 [part, specimen from Misanthla, Veracruz].

Hyla rickardsi Taylor, 1939a, p. 385 [holotype, F.M.N.H. No. 100077 (formerly E.H.T.-H.M.S. No. 5947) from Potrero Viejo, Veracruz, México; Edward H. Taylor and Dyfrig Forbes collectors]. Smith and Taylor, 1948, p. 85.

DIAGNOSIS: This medium-sized gray or tan frog with an extensive axillary membrane is characterized by an acutely rounded snout, angular canthus, and yellow webbing. This combination of characters readily distinguishes *godmani* from *loquax*, which has a blunt snout, rounded canthus, and red webbing. The only other Middle American hylid with an extensive axillary membrane is the small *Hyla ebraccata*, which has yellow thighs (pigmentless in preservative) and usually a contrasting pattern on the dorsum.

DESCRIPTION: Males of this medium-sized species attain a maximum snout-vent length of 38.0 mm. and females reach 36.6 mm. In a series of 25 males from Mata Oscura, Veracruz, México, the snout-vent length is 33.5 to 38.0 (mean, 35.6) mm.; the ratio of tibia length to snout-vent length is 0.496 to 0.529 (mean, 0.512); the ratio of foot length to snout-vent length is 0.421 to 0.463 (mean, 0.443); the ratio of head length to snout-vent length is 0.283 to 0.333 (mean, 0.296); the ratio of head width to snout-vent length is 0.312 to 0.349 (mean, 0.331), and the ratio of the diameter of the tympanum to that of the eye is 0.455 to 0.645 (mean, 0.552). Four females from the same locality have snout-vent lengths of 32.2 to 36.6 (mean, 35.0) mm.; the females do not differ significantly in any proportion from the males.

The head is slightly wider than long but narrower than the body. The top of the head is flat, and the eyes are prominent. In dorsal profile the snout is acutely rounded; in lateral profile it is bluntly rounded. The snout is moderately short; the nostrils are barely pro-

tuberant and situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is barely angular, but distinct; the loreal region is barely concave, and the lips are moderately thick but not flared. A thin dermal fold extends posteriorly from the orbit, above the tympanum, and to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about two-thirds of the diameter of the tympanum.

The arms are moderately long and slender; an extensive axillary membrane terminates on the posterior surface of the arm at a point about three-fourths of the distance from the axilla to the elbow. Tubercles are absent on the ventrolateral surface of the forearm, but a thin transverse dermal fold is present on the wrist. The fingers are moderately long and bear large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are large and conical; none is bifid. The supernumerary tubercles are moderately large and conical; they are present only on the proximal segments of each digit. The palmar tubercle is large, flat, and partially bifid. The prepollex is moderately enlarged and in breeding males lacks a horny nuptial excrescence. The fingers are about one-half webbed (fig. 172A). The webbing extends from the distal end of the antepenultimate phalanx of the first finger to the middle of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, and from the distal end of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A thin transverse dermal fold is present on the heel. In some specimens, a weak tarsal fold is present distally, but in most individuals the tarsal fold is absent. The inner metatarsal tubercle is elongately oval, flat, and barely visible from above. The outer metatarsal tubercle is small

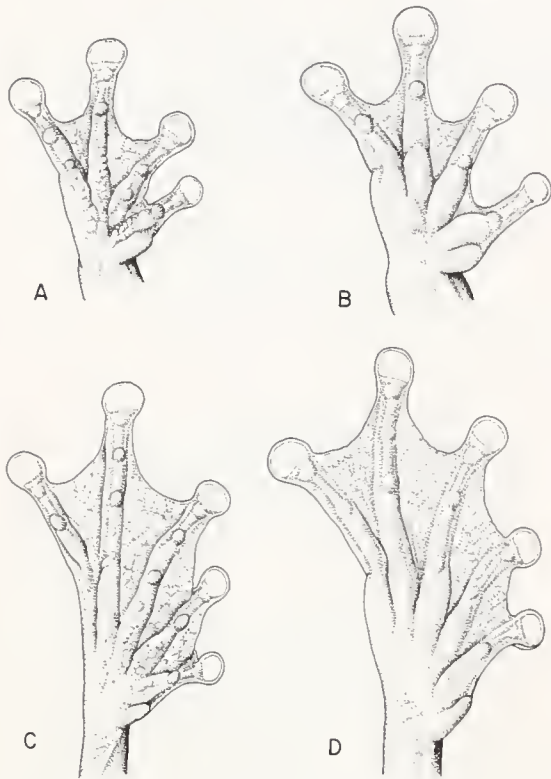


FIG. 172. Hands and feet of members of the *Hyla godmani* group. A and C. *Hyla godmani*, K.U. No. 64961. B and D. *Hyla loquax*, K.U. No. 103686. $\times 3$.

and subconical. The toes are moderately long and have discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately large and round. Small, subconical supernumerary tubercles are present on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 172C). The webbing extends from the distal end of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the base of the disc of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the level of the upper edges of the thighs; a short anal sheath is present. Numerous small tubercles are present below the anal opening. In general appearance the skin on

the dorsum is smooth, but under magnification it is minutely corrugated. The skin on the throat and ventral surfaces of the limbs, except the thighs, is smooth; that on the belly and ventral surfaces of the thighs is granular. The tongue is small, ovoid, or broadly cordiform with a shallow notch behind and barely free posteriorly. The dentigerous processes of the prevomers are posteromedially inclined elevations that are broadly separated medially and situated between the moderately large ovoid choanae. Males have four to six teeth on each process and a total of eight to 12 (mean, 10.2) prevomerine teeth. Females have three to six teeth on each process and a total of seven to 11 (mean, 9.3) prevomerine teeth. The vocal slits are long and extend along the inner edge of the lower jaws from a point opposite the base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration is uniform or faintly mottled gray, tan, or yellowish brown above and yellow below (pl. 55, fig. 3). When calling or active at night, individuals usually are a pale yellowish tan above. By day, the dorsal coloration changes to pale grayish tan or pale brown, or in some specimens, remains the same. Dark green, brown, or black flecks are present on the dorsum; in some specimens, paler tan or gray spots also are apparent during the day. Posterior surfaces of the thighs are dull yellow. The venter is pale lemon yellow, and the vocal sac is slightly duller yellow. The iris is dull bronze with a slight reddish tinge.

In some individuals, distinct transverse dark marks are present on the forearms and shanks. In some specimens, these marks consist of a series of short dashes or small spots, whereas in others distinct transverse bars are present. In the latter case, usually every other bar is about twice as wide as the intervening dark bars. Metachrosis is extreme in this frog; the change in coloration in a given individual encompasses the entire range of variation known in the species.

In preservative, the dorsum varies from pale grayish white to creamy tan or pale brown. In most specimens, some dark flecks, spots, or reticulations are present on the back. The posterior surfaces of the thighs are pale



FIG. 173. Tadpoles of members of the *Hyla godmani* group. A. *Hyla godmani*, K.U. No. 104185. B. *Hyla loquax*, K.U. No. 68379. $\times 3$.

creamy tan, and the flanks are creamy white. In most males, the anterior part of the chin is suffused with brown. A moderately broad white anal stripe is present in most specimens; likewise, a narrow white line usually is present on the outer edge of the foot. In some individuals small white spots are present on the flanks.

TADPOLES: A typical tadpole in developmental stage 38 has a total length of 35.5 mm. and a body length of 13.3 mm. The body is as wide as deep. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is sloping from the nostril to the mouth. The eyes are large and directed laterally. The nostrils are directed anterolaterally at a point about two-thirds of the distance from the eyes to the tip of the snout. The opening of the sinistral spiracle is below the midline at a point about two-thirds of the length of the body. The caudal musculature is moderately slender and reaches nearly to the tip of the tail. The caudal fins are moderately deep; at midlength of the tail, the depth of the caudal musculature is less than that of either fin. The dorsal fin barely extends onto the body (fig. 173A).

In life the body and caudal musculature are pale olive-gray; the caudal fins are transparent, and the entire tail is heavily reticulated with black. In preservative the body is pale olive-gray, and the caudal musculature is pale creamy tan. The reticulations on the tail are dark brown.

The mouth is anteroventral and moderately small; the width of the mouth is about one-

half of the greatest width of the body. The lips are folded laterally, and the median half of the upper lip is bare. Otherwise, the lips are bordered by two or three rows of small papillae; additional papillae are present in the lateral fold. The beaks are moderately slender and bear small serrations. The upper beak forms a broad arch with slender lateral processes that are moderately expanded distally. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth; all of the teeth are moderately long and slender. The two upper rows are equal in length and extend nearly to the edges of the lips. The second upper row is narrowly interrupted medially. The first and second lower rows are about equal in length to the upper rows, but the third lower row is noticeably shorter and bears smaller teeth. In some specimens, the first lower row is narrowly interrupted medially, whereas in others the first row is complete (fig. 174A).

MATING CALL: The call of *Hyla godmani* is a moderately high-pitched, pulsed note. The note repetition rate varies from 15 to 23 (mean, 18) notes per minute. The duration of each note is 0.15 to 0.20 (mean, 0.17) of a second. The pulse rate varies from 58 to 62 (mean, 60.2) pulses per second and the dominant frequency varies from 2780 to 3040 (mean, 2920) cycles per second. Three or four harmonics above the dominant frequency and one harmonic below the dominant frequency are emphasized in this well-modulated note (pl. 17, fig. 1).

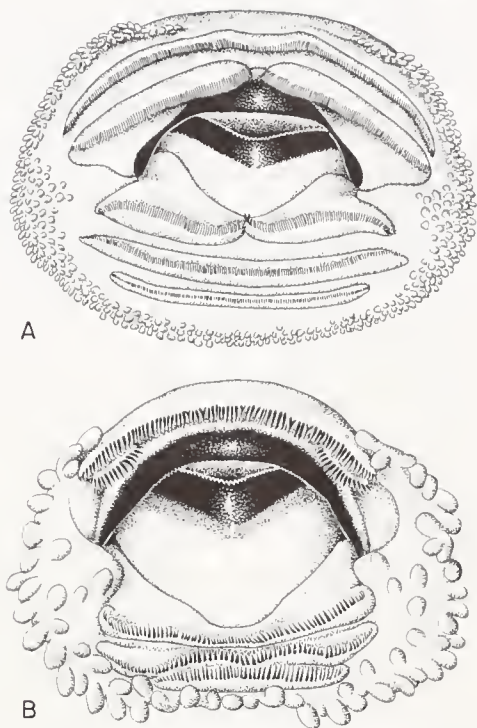


FIG. 174. Mouths of tadpoles of the *Hyla godmani* group. A. *Hyla godmani*, K.U. 104185. B. *Hyla loquax*, K.U. No. 68379. $\times 20$.

NATURAL HISTORY: *Hyla godmani* inhabits broad-leafed, evergreen forests in areas where there is a noticeable dry season. In the rainy months, frogs of this species congregate around temporary ponds in, or at the edge, of forested areas. At a pond 7 kilometers east-southeast of Córdoba, Veracruz, México, males of this species were observed calling from small trees, bushes, and clumps of grass around the pond, and from vegetation in the pond.

Tadpoles were found in a deep weedy pond, where they took refuge amidst the aquatic vegetation. One nearly metamorphosed individual has a snout-vent length of 12.2 mm. and a tail stub of 5.1 mm.

REMARKS: Duellman (1964c, p. 455) discussed the taxonomic status of the names *Hyla godmani* and *Hyla rickardsi*. Examination of the syntypes of *Hyla godmani* revealed that the series was composite and consisted of a single specimen of what is now *Hyla godmani* and eight specimens of *Hyla miotympanum* Cope. Duellman selected B.M.N.H. No. 1901.12.19.96 from the Misantla, Veracruz,

México, as the lectotype. This action relegated *Hyla rickardsi* Taylor (1939a) to the synonymy of *Hyla godmani* Günther [1901 (1855-1902)].

ETYMOLOGY: The specific name *godmani* is a patronym for Frederick D. Godman, one of the chief contributors to the British Biological Expedition of México and Central México in the Nineteenth Century.

DISTRIBUTION: *Hyla godmani* occurs on the coastal lowlands of Veracruz and southward in the foothills to elevations of about 900 meters in central Veracruz, México (fig. 175).

See Appendix 1 for the locality records of the 256 specimens examined.

Hyla loquax Gaige and Stuart

Hyla loquax Gaige and Stuart, 1934, p. 1 [holotype, U.M.M.Z. No. 75446 from Ixpuc Aguada, north of La Libertad, El Petén, Guatemala; Laurence C. Stuart collector]. Smith and Taylor, 1948, p. 84. Taylor, 1952c, p. 868. Duellman, 1960b, p. 62 [synonymized *Hyla axillamembrana* Shannon and Werler, 1955, with *Hyla loquax*]. Stuart, 1963, p. 36. Duellman, 1966b, p. 271 [synonymized *Hyla stadelmani* Schmidt, 1936, with *Hyla loquax*].

Hyla stadelmani Schmidt, 1936, p. 45 [holotype, M.C.Z. No. 21310 from the Subirana Valley, Departamento Yoro, Honduras; Raymond E. Stadelman collector].

Hyla axillamembrana Shannon and Werler, 1955, p. 383 [holotype, U.I.M.N.H. No. 67059 (formerly F.A.S. No. 4083) from 8 kilometers south of Lago de Catemaco on San Andrés Tuxtla-Minatitlán road, Veracruz, México; John Werler and Jack Reid collectors].

DIAGNOSIS: This medium-sized yellow or brown frog with an extensive axillary membrane is characterized by a blunt snout, rounded canthus, and bright red webbing and posterior surfaces of the thighs. *Hyla godmani* differs by having a more acuminate snout, angular canthus, yellow webbing, and tan posterior surfaces of the thighs. Only two other Middle American hylids have red webbing—*Hyla rufitela* and *H. pseudopuma infucata*. The former has a green dorsum and a prepollical spine in males and lacks an axillary membrane and red on the thighs. The latter has a blotched dorsal pattern, long snout, and large nuptial excrescences in males and lacks an axillary membrane. Juveniles of *Smilisca cyanosticta* have red on the posterior surfaces of the thighs but lack an axillary membrane.

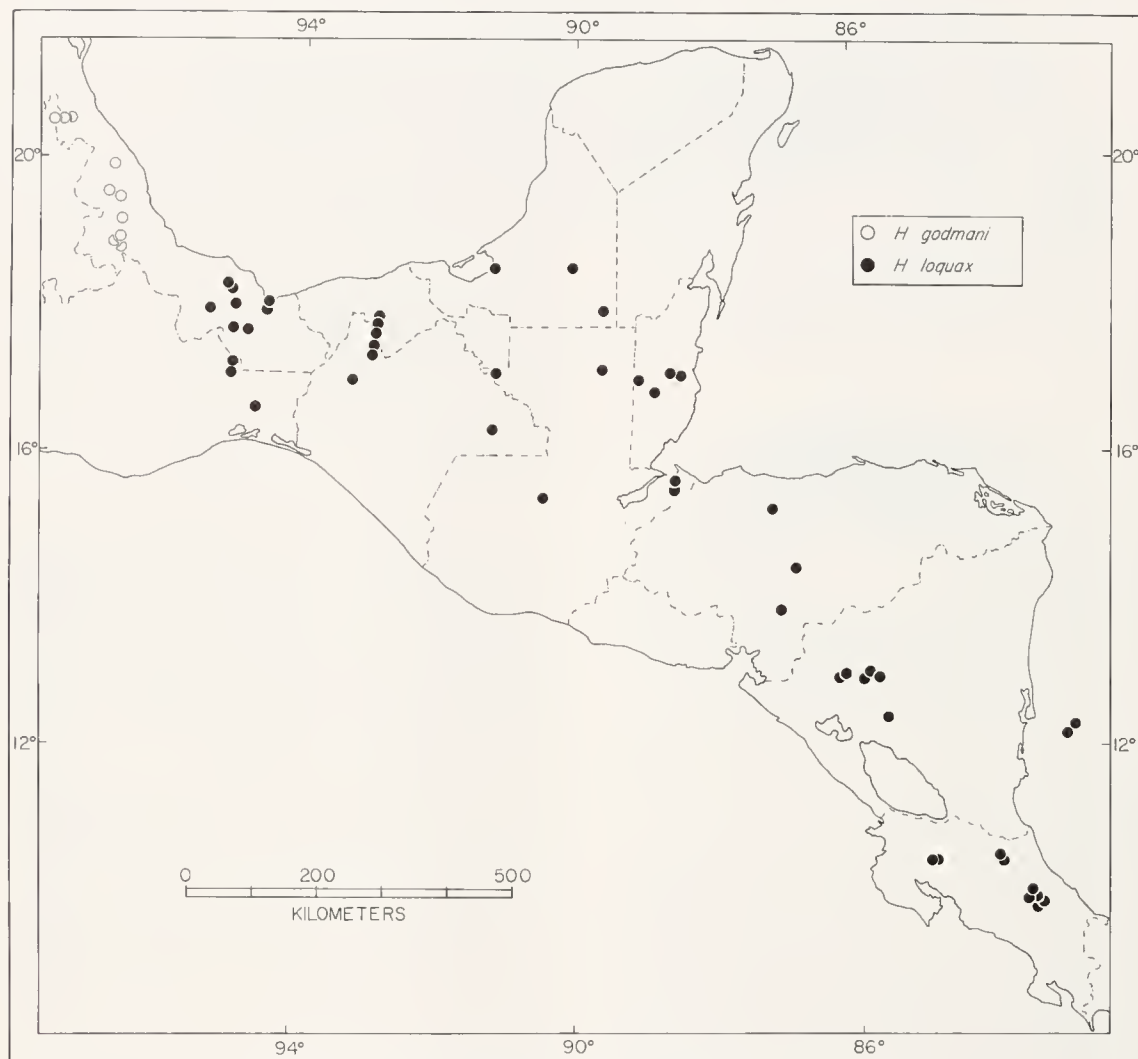


FIG. 175. Distribution of *Hyla godmani* and *Hyla loquax*.

DESCRIPTION: Males of this medium-sized species attain a maximum snout-vent length of 44.7 mm., and females reach 41.7 mm. In a series of 25 males from central El Petén, Guatemala, the snout-vent length is 35.9 to 43.4 (mean, 39.3) mm.; the ratio of tibia length to snout-vent length is 0.472 to 0.537 (mean, 0.510); the ratio of foot length to snout-vent length is 0.410 to 0.454 (mean, 0.435); the ratio of head length to snout-vent length is 0.290 to 0.327 (mean, 0.307); the ratio of head width to snout-vent length is 0.336 to 0.377 (mean, 0.357), and the ratio of the diameter of the tympanum to that of the eye is 0.512 to 0.694 (mean, 0.607). Four

females from the same locality have snout-vent lengths of 38.8 to 41.7 (mean, 40.5) mm. Specimens from the southern part of the range are slightly larger and have proportionately shorter legs and feet and proportionately smaller tympani. For example, in a series of 25 males from Turrialba, Cartago Province, Costa Rica, the snout-vent length is 33.8 to 44.7 (mean, 40.8) mm.; the ratio of tibia length to snout-vent length is 0.436 to 0.519 (mean, 0.482); the ratio of foot length to snout-vent length is 0.404 to 0.458 (mean, 0.424), and the ratio of the diameter of the tympanum to that of the eye is 0.383 to 0.590 (mean, 0.496).

The head is slightly wider than long, but slightly narrower than the body. The top of the head is flat, and the eyes are large and prominent. In dorsal profile, the snout is bluntly rounded, and in lateral profile it is round. The snout is short; the nostrils are slightly protuberant and situated at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is round and indistinct; the loreal region is not concave and the lips are thick and not flared. A thin dermal fold extends posteriorly from the orbit, above the tympanum, to a point above the insertion of the arm. The fold covers the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about one-half the diameter of the tympanum.

The arms are moderately long and robust; an extensive axillary membrane extends to the elbow. Distinct tubercles are absent on the ventrolateral edge of the arm, but a weak transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear moderately large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are moderately large and round; none is bifid. The supernumerary tubercles are small and numerous on the proximal segments of each digit. An elevated, tripartite palmar tubercle is present. The prepollex is moderately enlarged, and nuptial excrescences are absent in breeding males. The fingers are about two-thirds webbed (fig. 172B). The webbing extends from the base of the penultimate phalanx of the first finger to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the middle of the penultimate phalanx of the fourth finger. The legs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A strong, transverse dermal fold is present on the heel, and a weak tarsal fold is present distally on the tarsus. The inner metatarsal tubercle is moderately small, elliptical, and

barely visible from above. A small subconical outer metatarsal tubercle is present. The toes are moderately long and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately small and conical and the supernumerary tubercles are small, subconical, and numerous on the proximal segments of the digits. The toes are nearly fully webbed (fig. 172D). The web extends from the base of the disc of the first toe to the base of the second and on to the distal end of the penultimate phalanx of the third, from the base of the disc of the third to the distal end of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the level of the upper surfaces of the thighs. A short, granular anal sheath is present, and many large granules are present below the anal opening. The skin on the upper surfaces is smooth, but under magnification it is minutely corrugated. The skin on the throat and ventral surfaces of the limbs, except the thighs, is smooth, whereas that on the belly and ventral surfaces of the thighs is granular. The tongue is round or broadly cordiform and shallowly notched behind. Posteriorly the tongue is free for about one-fourth of its length. The dentigerous processes of the prevomers are narrowly separated transverse ridges between the moderately small, ovoid choanae. Individuals of both sexes have four to six teeth on each process and a total of eight to 12 prevomerine teeth. The average number of teeth in males is 10.3, and in females, 10.0. The vocal slits are long and extend along the inner edge of the lower jaw from the level of the base of the tongue to the angles of the jaws. The vocal sac is median, subgular, and moderately distensible.

The general coloration of *Hyla loquax* is dull reddish brown, yellowish tan, or pale gray above with bright red webs and hidden surfaces of the thighs (pl. 55, fig. 5). Usually at night the dorsum is pale tan or pale reddish brown. Small dark brown or olive-brown flecks usually are present on the back and dorsal surfaces of the limbs; there are no transverse bars on the limbs. The venter is creamy yellow. The axilla, groin, and anterior and posterior surfaces of the thighs,

inner surfaces of the tarsi, the first through third toes, and the webbing on the hands and feet are tomato red. The iris is a dull reddish tan.

Some individuals change from the color described above to a darker brown with olive-brown irregular markings on the dorsum. By day, most individuals are pale gray, almost white. However, the red on the thighs and webbing, and in the axilla and groin remains constant.

In preservative the dorsum varies from uniform dull reddish brown to uniform grayish white or these same ground colors with darker flecks. The anterior and posterior surfaces of the thighs, the axilla and groin, and the webbing is creamy yellow. The ventral surfaces are creamy white. A thin white anal stripe is present in some individuals, whereas in others there is no anal marking, and in some specimens the entire anal area is white.

TADPOLES: A typical tadpole in developmental stage 26 has a body length of 11.2 mm. and a total length of 27.5 mm. The body is as deep as wide; the snout is rounded in dorsal and lateral profiles. The eyes are moderately large and directed laterally. The nostrils are directed anterolaterally and situated at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is at the midline about midlength on the body. The anal tube is short and dextral. The caudal musculature is relatively thin and extends nearly to the tip of the tail. The caudal fins are moderately deep, and the dorsal fin extends onto the body. At midlength of the tail the depth of the caudal musculature is slightly less than either the dorsal or ventral fin (fig. 173B).

In preservative, the body is pale olive-tan, and the caudal musculature is creamy tan. The fins are transparent; the entire tail is marked with fine brown flecks and reticulations.

The mouth is anteroventral; its width is equal to about half of the greatest width of the body. The lips are folded laterally, and the median part of the upper lip is bare. The rest of the lips are bordered by one row of large, blunt papillae. In the lateral fold, additional large papillae are present. The beaks

are moderately heavy and bear pointed serrations. The upper beak forms a broad arch lacking lateral processes. The lower beak is broadly V-shaped. There are two upper and three lower rows of teeth; all of the teeth are long, pointed, and heavy at the base. The upper tooth rows extend to the edges of the lips, and the second upper tooth row is broadly interrupted medially. The lower tooth rows are complete and the third lower tooth row is much shorter than the others (fig. 174B).

MATING CALL: The call of *Hyla loquax* consists of a series of notes sounding much like the honking of a goose. Notes are repeated at intervals of slightly less than one second to about five seconds. The note repetition rate varies from nine to 62 (mean, 31) notes per minute. The duration of the notes is 0.05 to 0.16 (mean, 0.095) of a second. The pulse rate is 100 to 150 (mean, 129) pulses per second and the dominant frequency is 2180 to 2430 (mean, 2323) cycles per second (pl. 16, fig. 3). In these poorly modulated notes, there is no emphasized harmonic above the dominant frequency; the energy is rather evenly spread throughout the frequency spectrum.

NATURAL HISTORY: *Hyla loquax* inhabits lowland, humid tropical forest and breeds in temporary ponds in, or at the edge of the forest. Males sometimes call from bushes or large herbs at the edge of, or in the water, but most frequently males are found on leaves of floating vegetation, such as water lilies. Usually the calling sites are away from shore and in deep water.

The eggs are deposited in large gelatinous masses attached to aquatic vegetation; one clutch examined contained about 250 eggs. The tadpoles are exceedingly wary and apparently remain in deep water where there is some submerged vegetation.

REMARKS: Shannon and Werler (1955, p. 383) named *Hyla axillamembrana* from southern Veracruz, México. Duellman (1960b, p. 60) demonstrated that *axillamembrana* (known only from the type specimen) was actually *Hyla loquax*. The status of *Hyla stadelmani* Schmidt had been questioned by several authors; Duellman (1966b, p. 271) reported upon the comparison of freshly preserved specimens of *Hyla loquax* and para-

types of *Hyla loquax* with the holotype of *Hyla stadelmani*; he concluded that *Hyla stadelmani* is a synonym of *Hyla loquax*.

The distribution of *Hyla loquax* in comparison with that of *Hyla godmani* offers an apparent excellent example of ecological and geographic replacement. In the northern part of its range, *Hyla godmani* occurs on the coastal lowlands; southward where its range approaches that of *loquax*, *godmani* occurs only in the foothills. In southern Veracruz, where the ranges of the two species are closest, *Hyla loquax* occurs on the lowlands. In Nicaragua and Costa Rica this species occurs on the lowlands, but it seems to reach its greatest abundance in the foothills.

ETYMOLOGY: The specific name is Latin meaning talkative or garrulous and refers to the incessant calling characteristic of this species.

DISTRIBUTION: *Hyla loquax* occurs in forested areas on the Caribbean lowlands and foothills from southern Veracruz, México, southeastward to Costa Rica (fig. 175). In Nicaragua and Costa Rica, the species has been found at several localities at elevations above 1000 meters.

See Appendix 1 for the locality records of the 665 specimens examined.

The *Hyla picta* Group

DEFINITION: Members of this group are small pond-breeding species; males attain a maximum snout-vent length of 26.0 mm. and females, 31.0 mm. The dorsum is yellow or tan with or without brown flecks, and a white dorsolateral stripe is present. The thighs are deep yellow. The palpebral membrane is clear. The hands are only about one-fourth webbed, and the feet are no more than two-thirds webbed. A tarsal fold and dermal appendages are lacking, but an axillary membrane is present. Males have a single, median, subgular vocal sac and horny nuptial excrescences on the prepollices. The skulls are weakly ossified, and a large frontoparietal fontanelle is present (fig. 176). The nasals are moderately well developed and separated medially. The sphenethmoid is poorly ossified. The squamosal is not in bony contact with the crista parotica, and the anterior arm of the squamosal extends about one-third of

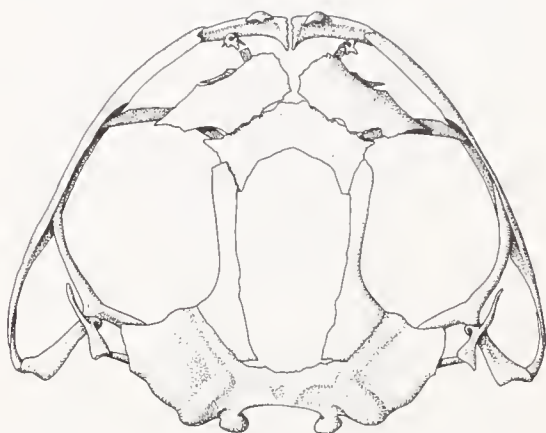


FIG. 176. Dorsal view of the skull of *Hyla smithii*, K.U. No. 59923. $\times 7$.

the distance to the maxillary. The quadratojugal is in bony contact with the maxillary. The prevomers are poorly ossified, do not articulate with surrounding bones, and bear teeth (*smithii*) or not (*picta*). The medial ramus of the pterygoid does not articulate with the prootic. The known tadpoles have deep, terminally pointed fins and small anteroventral mouths with two upper and three lower rows of teeth. The mating calls consist of a series of rapidly produced, well-modulated, short, high-pitched notes. The haploid number of chromosomes is 12.

COMPOSITION: Two species (*picta* and *smithii*) comprise the group, which occurs at low to moderate elevations in México and northern Central America. Of the two species, 2714 preserved frogs, eight skeletons, three lots of tadpoles, and one preserved clutch of eggs have been examined.

COMMENTS: The two species certainly seem to be closely related on the basis of external characters and on the nature of the mating calls. *Hyla picta* is smaller than *smithii* but has slightly more webbing (fig. 177). The skulls of the two species differ slightly. In *picta*, the nasals have incomplete maxillary processes and articulate with the sphenethmoid, whereas in *smithii* maxillary processes are lacking, and the nasals do not articulate with the sphenethmoid. Furthermore, minor differences exist in the shapes of the septomaxillaries.

Fouquette (1961b) pointed out the allo-

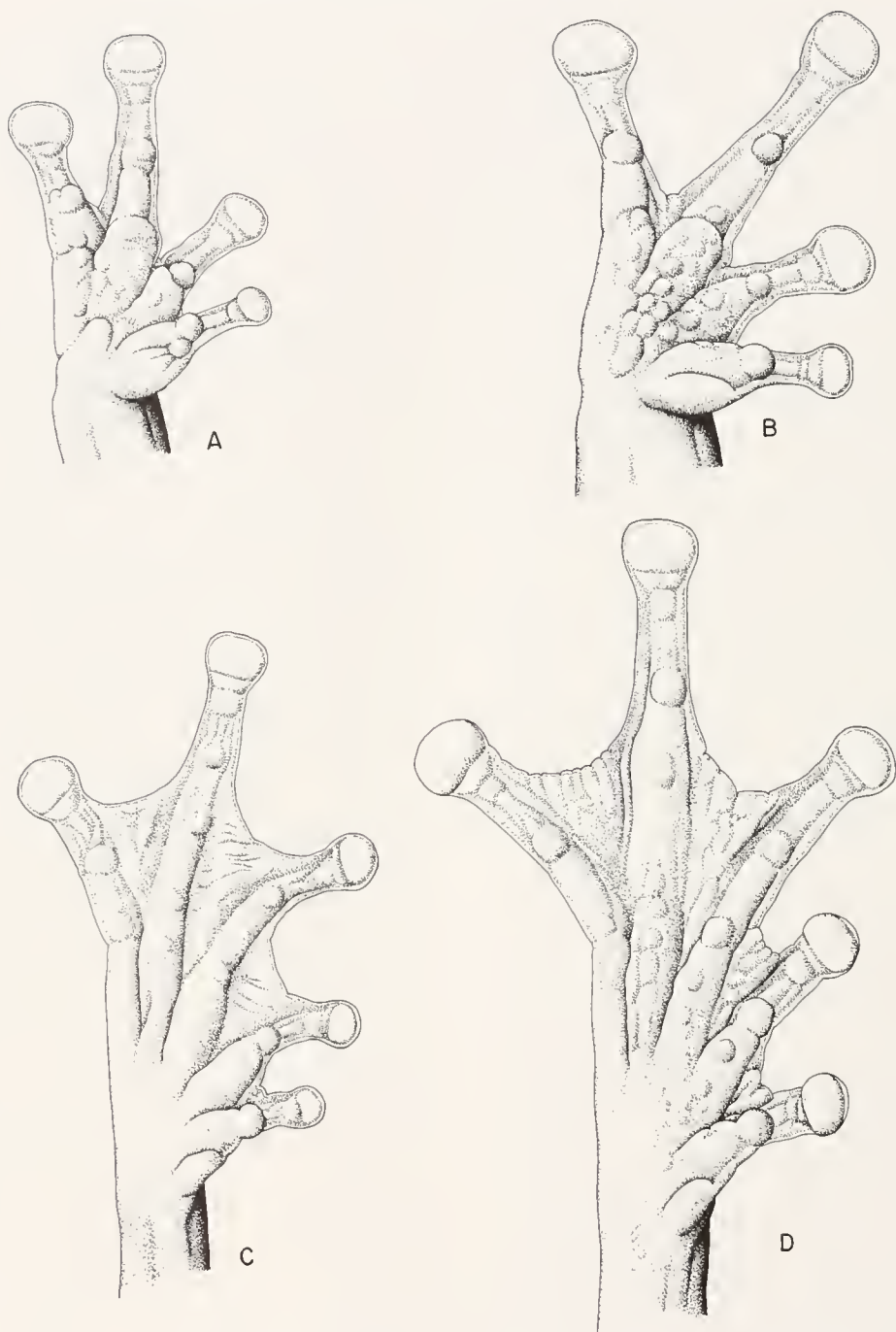


FIG. 177. Hands and feet of members of the *Hyla picta* group. A and C. *Hyla picta*, K.U. No. 57599. B and D. *Hyla smithii*, K.U. No. 57702. $\times 8$.

patric ranges of the two species and noted that: "The calls of *smithii* and *picta*, though basically similar, differ in several important characteristics, to a degree that has been

shown to be effective in isolating other sympatric hylid species." The geographical barrier separating the ranges of the two species is the arid Pacific lowland region in the Isth-

mus of Tehuantepec. *Hyla smithii* occurs northwestward from the isthmus on the Pacific lowlands of México, whereas *Hyla picta* is on the Atlantic lowlands.

Duellman and Fouquette (1968) pointed out the superficial similarities between members of the *picta* and *microcephala* groups of *Hyla*. Both are small yellowish tan frogs with similar kinds of mating calls. However, frogs in the *microcephala* group differ by having no quadratojugal, tadpoles with xiphicereal tails and terminal mouths lacking teeth, and a haploid number of 15 chromosomes. In all of these characteristics, frogs of the *microcephala* group seem to be allied with the South American *leucophyllata* and *parviceps* groups rather than with the *picta* group. Although differing greatly in size and in the sound (but not structure) of the mating calls, the frogs in the *picta* group might be most closely related to the *Hyla loquax* group on the Atlantic lowlands of México and Central America. Frogs in both groups have similar cranial features and larval characteristics.

Hyla picta (Günther)

Hylella picta Günther, 1901 (1885-1902), p. 286 [holotype, B.M.N.H. No. 1947.2.22.62 from Jalapa, Veracruz, México; Mateo Trujillo collector]. Kellogg, 1932, p. 180.

Hyla picta: Nieden, 1923, p. 284. Smith and Taylor, 1948, p. 85. Stuart, 1963, p. 36.

DIAGNOSIS: This small yellow frog has a brown lateral stripe, bordered above by a white line, extending from the tip of the snout to the middle of the flank. Numerous brown flecks usually are present on the back, and distinct brown flecks are present on the forearms and shanks. It most closely resembles *Hyla smithii* which is larger (males to 26 mm., as opposed to 21.4 mm. in *picta*) and has prevomerine teeth (lacking in *picta*). Furthermore, in *smithii* the dark flecks, if present on the forearms and shanks, are indistinct. Other small yellow Middle American hylids having uniformly yellow thighs have irregular dark reticulations on the back (*microcephala underwoodi* and *phlebodes*), dark chevrons on the back (*sartori*), a dark hourglass or pair of triangles on the back (*ebraccata*), a pair of dark paravertebral lines (*microcephala microcephala*), a broad dark lateral stripe extend-

ing to the groin (*robertmertensi*), or no lateral stripe bordered above by a white line (*sumichrasti*).

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 21.4 mm., and females reach 22.1 mm. In a series of 25 males from southern Campeche, México, and El Petén, Guatemala, the snout-vent length is 18.6 to 21.4 (mean, 20.2) mm.; the ratio of tibia length to snout-vent length is 0.471 to 0.536 (mean, 0.494); the ratio of foot length to snout-vent length is 0.383 to 0.430 (mean, 0.409); the ratio of head length to snout-vent length is 0.316 to 0.347 (mean, 0.328); the ratio of head width to snout-vent length is 0.321 to 0.355 (mean, 0.340), and the ratio of the diameter of the tympanum to that of the eye is 0.318 to 0.458 (mean, 0.406). Females do not differ from males in proportions.

The head is slightly narrower than the body, and the top of the head is flat. In dorsal and lateral profiles, the snout is rounded. The snout is moderately long; the nostrils are barely protuberant and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is nearly flat; the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance slightly greater than the diameter of the tympanum.

The arm is moderately short and slender; a distinct axillary membrane is present. Tubercles are lacking on the ventrolateral edge of the forearm, but a weak transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear small discs; the width of the disc on the third finger is slightly less than the diameter of the tympanum. The subarticular tubercles are large and ovoid; none is bifid. The supernumerary tubercles are low, rounded elevations on the proximal segments of the digits. A low, flat palmar tubercle is present. The prepollex is barely enlarged and in breeding males bears a weak nuptial excrescence. The

fingers are about one-third webbed (fig. 177A). The webbing is vestigial between the first and second finger, and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from the distal end of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A distinct transverse dermal fold is present on the heel, and a low tarsal fold is present distally on the tarsus. The inner metatarsal tubercle is low, rounded, and ovoid. No outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are as large as those on the fingers. The subarticular tubercles are moderately large and ovoid; the supernumerary tubercles are low and subconical. The toes are about three-fourths webbed (fig. 177C). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. A short, broad anal sheath is present, but tubercles beside the anal opening are lacking. The skin on the throat, belly, and proximal postero-ventral surfaces of the thighs is weakly granular; elsewhere, the skin is smooth. The tongue is cordiform, moderately notched behind, and free posteriorly for about one-fourth of its length. Dentigerous processes are lacking on the prevomers. The choanae are moderately large and ovoid. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla picta* is pale yellowish tan with dark brown flecks on the dorsum and a dorsolateral light stripe

(pl. 55, fig. 4). Usually the dorsal ground color is pale tan. Numerous dark brown flecks or small spots are present on the back, and brown flecks are present on the dorsal surfaces of the forearms, shanks, and feet. A creamy white dorsolateral stripe extends from the tip of the snout, through the nostril and eye, to the middle of the flank. This narrow stripe is bordered by a brown stripe. The ventral surfaces are creamy white, and the vocal sac is yellow. The thighs are uniformly yellowish tan or yellow with minute tan flecks. The iris is pale bronze.

Some individuals when active at night are nearly uniformly pale yellowish tan; in these frogs the dorsolateral stripes are not evident. By day, the pattern has more contrast.

In preservative, the dorsal ground color varies from pale yellowish tan to pale reddish brown. Dark spots on the dorsum and limbs are dark brown. Usually the dorsolateral light stripe is evident and bordered below by a noticeable brown stripe. The ventral surfaces are dull creamy tan.

TADPOLES: A small series of tadpoles is available from 5 kilometers south-southwest of Chiltepec, Oaxaca, México. A typical tadpole in developmental stage 38 has a body length of 9.5 mm. and a total length of 28.0 mm. The body is noticeably deeper than wide; the snout is bluntly rounded in both dorsal and lateral profile. The eyes are moderately large, widely separated, and directed laterally. The nostrils are protuberant at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posteriorly below the midline at a point about two-thirds of the distance from the tip of the snout to the posterior end of the body. The cloacal tube is short and dextral. The caudal musculature is moderately slender and extends to the tip of the pointed tail. The fins are deep, and the dorsal fin extends onto the body. At mid-length of the tail, the depth of the caudal musculature is noticeably less than the depth of either fin (fig. 178).

The body and tail are pale creamy tan with small brown flecks on the dorsal surfaces of the body and on the caudal fins and musculature. A dark brown stripe extends from the



FIG. 178. Tadpole of *Hyla picta*, K.U. No. 104187. $\times 4$.

tip of the snout through the eye, which is pale bronze. In preservative the tadpoles are creamy white with scattered brown flecks on the dorsal surfaces of the body and on the fins and caudal musculature. The flecks tend to form vertically oriented bars on the distal half of the caudal musculature. A distinct brown stripe is present from the snout to the eye.

The mouth is small and anteroventral. The median part of the upper lip is bare; elsewhere, the lips are bordered by a single row of moderately large papillae. Lateral folds are present in the lips. The beaks are moderately robust and bear fine serrations. The upper beak is in the form of a broad arch with long slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth; all of the teeth are long. The second upper row is narrowly interrupted medially and is nearly as long as the first upper row, which extends to the margins of the lips. The lower rows are complete; the first and second lower rows are nearly as long as the upper ones, and the third lower row is noticeably shorter (fig. 179).

MATING CALL: The call of *Hyla picta* is an insect-like "creek-eeek-eeek-eeek." Notes are produced at a rate of 36 to 94 (mean, 64) notes per minute. The duration of each note varies from 0.033 to 0.075 (mean, 0.043) of a second, and there are 34 to 63 (mean, 53) pulses per second. The fundamental frequency is the dominant frequency and falls between 1676 and 3320 (mean, 2661) cycles per second. There are one or two harmonics emphasized above the fundamental frequency (pl. 19, fig. 1).

NATURAL HISTORY: *Hyla picta* inhabits tropical lowlands characterized by a distinct rainy season, at which time the frogs congre-

gate at shallow grassy pools for breeding. Males call from emergent vegetation and from low bushes. During the dry season, individuals have been found in bromeliads.

The tadpoles have been found in shallow weedy ponds, where the tadpoles seek refuge amidst the dense vegetation.

REMARKS: For many years this small frog was placed in the genus *Hylella*, a catch-all assembly of small hylids lacking prevomerine teeth.

ETYMOLOGY: The specific name is Latin, meaning painted, and evidently refers to the small spots on the dorsum.

DISTRIBUTION: *Hyla picta* ranges throughout the lowlands of Middle America up to elevations of 1300 meters from southern San Luis Potosí, México, to northern Honduras (fig. 180). It does not occur in exceedingly dry areas, such as the northern parts of the Yucatan Peninsula.

See Appendix 1 for the locality records of the 774 specimens examined.

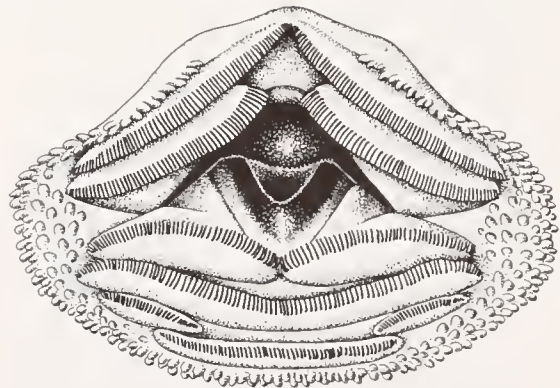
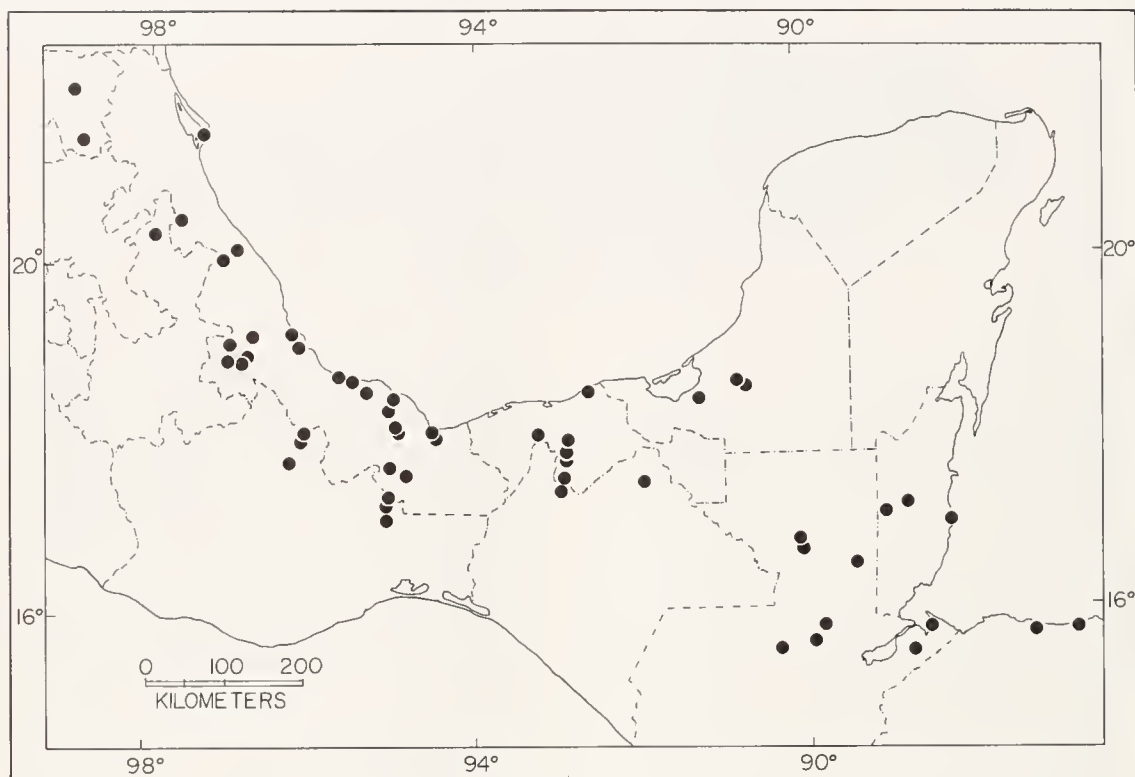


FIG. 179. Mouth of tadpole of *Hyla picta*, K.U. No. 104187. $\times 25$.

FIG. 180. Distribution of *Hyla picta*.

Hyla smithii Boulenger

Hyla nana Günther, 1901 (1885-1902), p. 263 [syntypes, B.M.N.H. Nos. 1947.2.12.76-82 from Cuernavaca, Morelos, México; Herbert H. Smith collector (not *Hyla nana* Boulenger, 1889, from Colonia Resistencia, Chaco, Argentina)].

Hyla smithii Boulenger, 1902b, p. 33 [replacement name for *Hyla nana* Günther, preoccupied]. Smith and Taylor, 1948, p. 85.

Hyla eximia (part): Kellogg, 1932, p. 164.

DIAGNOSIS: This small yellow frog has a white dorsolateral stripe extending from the tip of the snout to the mid-flank. The stripe usually is bordered below by a narrow brown line. The dorsum is yellow or tan, with or without small brown flecks. Indistinct brown flecks usually are present on the forearms and shanks. This species is similar to the smaller *Hyla picta* (males to 21.4 mm., as opposed to 26 mm. in *smithii*) but has less distinct markings, no wide brown lateral stripe, and prevomerine teeth (lacking in *picta*). Other small yellow Middle American hylids having uniformly yellow thighs have irregular dark

reticulations on the back (*microcephala underwoodi* and *phlebodes*), dark chevrons on the back (*sartori*), a dark hourglass or pair of triangles on the back (*ebraccata*); a pair of dark paravertebral lines (*microcephala microcephala*), a broad dark lateral stripe extending to the groin (*robertmertensi*), or no lateral stripe bordered above by a white line (*sumichrasti*).

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 26.0 mm., and females reach 30.8 mm. In a series of 25 males from La Candelaria, Oaxaca, México, the snout-vent length is 23.0 to 26.0 (mean, 24.3) mm.; the ratio of tibia length to snout-vent length is 0.472 to 0.550 (mean, 0.506); the ratio of foot length to snout-vent length is 0.402 to 0.458 (mean, 0.427); the ratio of head length to snout-vent length is 0.303 to 0.333 (mean, 0.312); the ratio of head width to snout-vent length is 0.316 to 0.359 (mean, 0.333), and the ratio of the diameter of the tympanum to that of the eye is 0.407 to 0.560 (mean, 0.480). Six females

from the same locality have snout-vent lengths of 27.4 to 30.8 (mean, 27.7) mm. They differ from the males by having a slightly larger tympanum; the ratio of the diameter of the tympanum to that of the eye is 0.462 to 0.607 (mean, 0.520). No significant differences in size or proportions are evident from measurements of samples throughout the range of the species.

The head is slightly narrower than the body, and the top of the head is flat. In dorsal profile, the snout is acutely rounded; in lateral profile, it is round. The snout is moderately long; the nostrils are protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is slightly angular, and the loreal region is nearly flat. The lips are barely thickened and not flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is only barely distinct and separated from the eye by a distance slightly less than the diameter of the tympanum.

The arms are moderately short and robust; a distinct axillary membrane is present. No tubercles are present on the ventrolateral edge of the forearm, but a thin transverse dermal fold is present on the wrist. The fingers are moderately short and robust and bear medium-sized discs; the width of the disc on the third finger is about equal to the diameter of the tympanum. The subarticular tubercles are large and subconical; none is bifid. The supernumerary tubercles are low, rounded, and present on the proximal segments of the digits. A flat, usually bifid palmar tubercle is present. The prepollex is only moderately enlarged and in breeding males bears a weak nuptial excrescence. The webbing on the fingers is vestigial (fig. 177B). The hind limbs are moderately short and robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibio-tarsal articulation extends to the middle of the eye. A weak transverse dermal fold is present on the heel, and a weak tarsal fold usually is evident distally on the tarsus. The inner metatarsal tubercle is small, flat, and ovoid. An outer metatarsal tubercle is lack-

ing. The toes are moderately long and slender and bear discs that are nearly as large as those on the fingers. The subarticular tubercles are moderately large and subconical, and the supernumerary tubercles are low, flat, and indistinct. The toes are about three-fourths webbed (fig. 177D). The webbing extends from the middle of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. A short, broad anal sheath is present, but tubercles are absent around the anal opening. The skin on the throat, belly, and proximal postero-ventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is cordiform, shallowly notched posteriorly, and free behind for about one-third of its length. The dentigerous processes of the prevomers are widely separated, transverse or postero-medially inclined elevations between the moderately large, ovoid choanae. Males have two or three teeth on each process and a total of four to six (mean, 5.1) prevomerine teeth; females have two to four teeth on each process and a total of five to seven (mean, 6.0) prevomerine teeth. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and greatly distensible.

The general coloration of *Hyla smithii* consists of a pale yellow or tan dorsum with a white or creamy yellow dorsolateral stripe (pl. 55, figs. 1 and 2). When active at night the dorsum usually is pale yellow, and a distinct lateral stripe extends from the tip of the snout, through the eye, to a point on the flanks. The thighs are uniformly yellow or yellowish tan; the belly is white, and the vocal sac is bright yellow. The iris is silvery bronze.

The coloration by day is highly variable. Some individuals are pale yellowish tan, whereas others are dark yellow or brown. The

dorsolateral stripe varies from white to pale yellow.

In preservative, the dorsum is yellowish tan to pale brown with or without small dark flecks. The dorsolateral stripe is creamy white. Most individuals have some faint dark markings on the shanks and forearms. The belly is white, and the other ventral surfaces are creamy tan.

TADPOLES: Some recently hatched tadpoles and metamorphosing young are available, but tadpoles in developmental stages possessing the diagnostic larval characters are lacking.

MATING CALL: The call of *Hyla smithii* consists of a series of insect-like chirping notes. Notes are produced at a rate of 60 to 72 (mean, 68) notes per minute. The duration of each note varies from 0.025 to 0.042 (mean, 0.032) of a second. The pulse rate varies from 30 to 48 (mean, 36) pulses per second. The fundamental frequency varies from 800 to 3100 (mean, 1033) cycles per second, and the dominant frequency, the second harmonic, varies from 1600 to 6200 (mean, 2066) cycles per second (pl. 19, fig. 2).

NATURAL HISTORY: *Hyla smithii* inhabits the subhumid Pacific lowlands of México, characterized by many months of little or no rain. In the rainy season, this small frog is virtually ubiquitous throughout the Pacific lowlands. Males can be heard calling from nearly any temporary pond or roadside ditch. Males usually call from emergent vegetation, but frequently the frogs call from low bushes. Apparently, this species also utilizes small, sluggish streams for breeding, because numerous males have been heard calling along such streams. By day and in the dry season, these frogs seek shelter in the axils of the leaves of elephant-ear plants (*Xanthosoma*).

REMARKS: Kellogg (1932, p. 165) stated: "The cotypes (B.M. Nos. 1901.12.19.76-82) of *Hyla nana* Günther (preoccupied=*Hyla smithii* Boulenger) are likewise referred to this species [*Hyla eximia*]. Dr. E. R. Dunn carefully examined a series of specimens of *H. eximia* with the cotypes of *H. nana* and concluded that this species was not valid. Conversely, H. W. Parker, who had previously examined the cotypes wrote that *H. smithii* seemed to differ from both *H. eximia* and *H.*

gracilipes." Taylor (1936, p. 357) redescribed *Hyla smithii*; since that time no one has confused this species with *Hyla eximia*.

In some samples of *Hyla smithii*, the prevomerine teeth are poorly developed. Oliver (1937, p. 6) stated that 14 of the 49 specimens from Colima completely lack vomerine teeth, and that in the remaining 35 the teeth were fully developed on both sides, partially developed on both sides, or absent on one side and present on the other. My observations corroborate those of Oliver, except that I find that most individuals do have dentigerous processes present on both sides. In many individuals the processes are low, and the teeth are completely hidden in the mucosa.

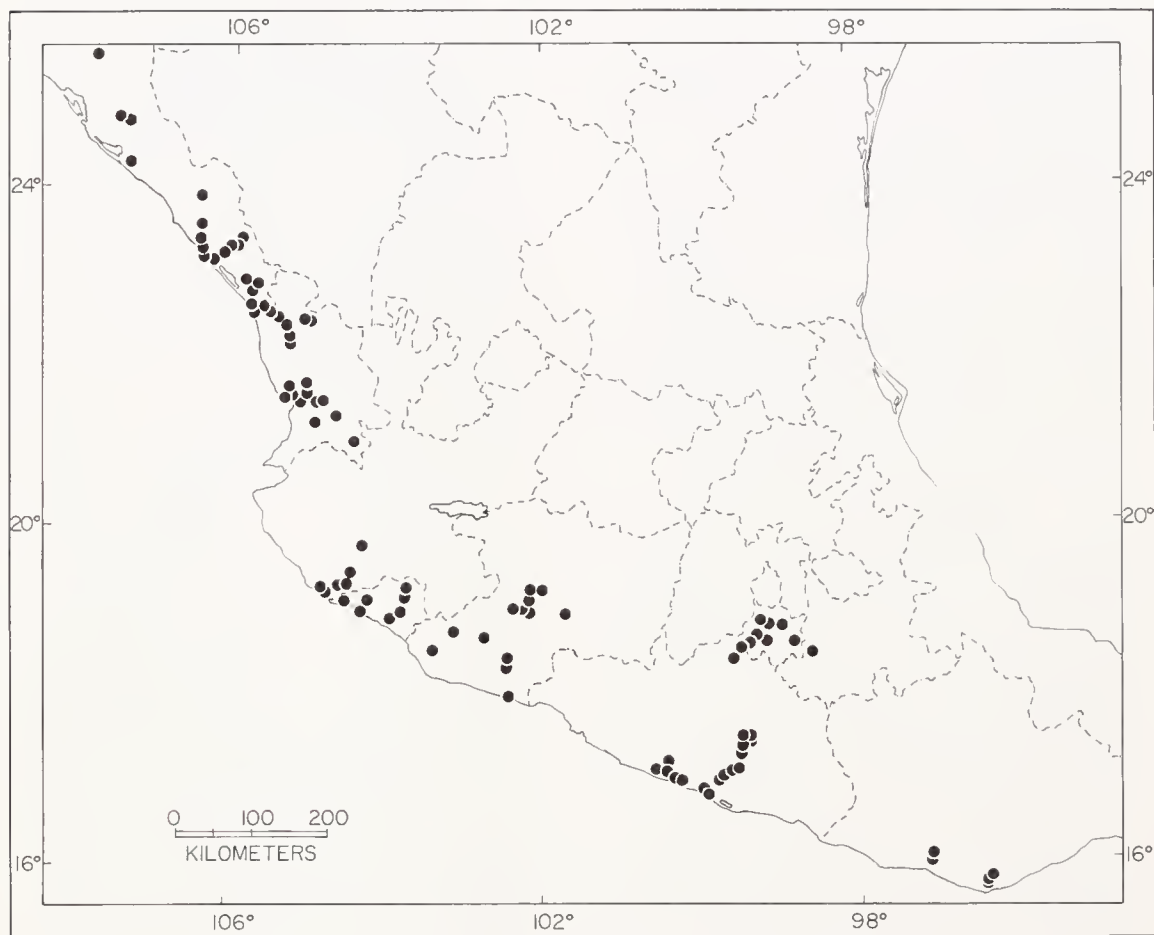
ETYMOLOGY: The specific name is a patronym for Herbert H. Smith, who collected the type series.

DISTRIBUTION: *Hyla smithii* occurs throughout the subhumid Pacific lowlands up to elevations of about 1000 meters from central Sinaloa to southern Oaxaca, México, and inland in the Balsas-Tepalcatepec Basin (fig. 181).

See Appendix 1 for the locality records of the 1952 specimens examined.

The *Hyla miotympanum* Group

DEFINITION: The members of this group are medium-sized, stream-breeding species; males attain a maximum snout-vent length of 38.4 mm. and females, 51.6 mm. The dorsum basically is pale green, but metachrosis results in the appearance of darker reticulations or mottling on a green or tan background. The anterior and posterior surfaces of the thighs are uniform brown, and the dorsal surfaces of the limbs are not marked by transverse bands. The palpebral membrane is clear. The fingers are no more than one-half webbed, and the feet are less than three-fourths webbed. Dermal fringes and appendages are absent on the limbs. A tarsal fold is present, but an axillary membrane is lacking. Males have single, median, subgular vocal sacs and horny nuptial excrescences on the pollices. The cranial elements are moderately well ossified; a large frontoparietal fontanelle is present. The sphenethmoid is large and extends anteriorly between the nasals me-

FIG. 181. Distribution of *Hyla smithii*.

dially (*arborescens*) or is small and lies posterior to the nasals (*miotympanum*). The nasals broadly overlap the sphenethmoid in *arborescens* and are narrowly separated from the sphenethmoid in *miotympanum* (fig. 182). The quadratojugal is absent. The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosal extends no more than half of the distance to the maxillary. The medial ramus of the pterygoid is not in bony contact with the prootic. Prevomerine teeth are present. The tadpoles have moderately long, terminally rounded tails and small mouths with lateral folds and two upper and three or four lower rows of teeth. The mating calls consist of a series of short, rather low-pitched notes. The haploid number of chromosomes is 12 and the diploid number is 24.

COMPOSITION: Two species (*arborescens* and *miotympanum*) comprise the group, which occurs on the Atlantic slopes from Nuevo León to Chiapas in México. Of the two species, 1811 preserved frogs, 27 skeletons, 20 lots of tadpoles, and three preserved clutches of eggs have been examined.

COMMENTS: *Hyla arborescens* and *miotympanum* are placed in the same group on the basis of similarities in cranial features and characters of the tadpoles. Externally, the adults of *Hyla erythromma* closely resemble those of *miotympanum*, but *erythromma* has a quadratojugal, and the tadpoles of that species have four upper and six lower rows of teeth.

Hyla arborescens might equally well be placed in the *Hyla bistincta* group, except that the members of the *bistincta* group that

most closely resemble *arborescens* lack vocal slits and a vocal sac. *Hyla arborescens* and *hazela* merely have external characteristics similar to those in members of the *Hyla bistincta* group, as well as the loss of the quadratojugal; apparently these similarities are the result of convergence or parallelism and are not indicative of close relationship.

Hyla miotympanum has a much broader geographic and altitudinal range than does *arborescens*, which possibly differentiated from the former at high elevations. The two species occur sympatrically in some areas at elevations of 1800 to 2200 meters.

Hyla miotympanum Cope

Hyla miotympanum Cope, 1863, p. 47 [syntypes, U.S.N.M. No. 6311 (now lost) and another specimen that apparently was never catalogued (*fide* Kellogg, 1932, p. 170) from Jalapa and Mirador, Veracruz, México; R. Montes de Oca and Charles Sartorius collectors]. Brocchi, 1882, p. 37. Boulenger, 1882a, p. 400. Günther, 1901 (1885-1902), p. 279. Kellogg, 1932, p. 170. Smith and Taylor, 1948, p. 90.

Hyla microtis Peters, 1869, p. 880 [syntypes, Z.M.B. No. 6657 (two specimens) from Puebla, México; Berkenbusch collector].

Hyla godmani (part) Günther, 1901 (1885-1902), p. 295 [specimens from Jalapa, Veracruz, México].

Hyla darlingi Smith, Smith, and Werler, 1952, p. 254 [holotype, U.I.M.N.H. No. 21903 from Xico, Veracruz, México; John E. Werler collector].

DIAGNOSIS: This moderately small green *Hyla* has the fingers about one-third, and the toes about three-fourths webbed. Distinct white stripes are present on the margin of the upper lip, above the anal opening, and on the outer edges of the forearms and feet. There are no transverse bands on the limbs. *Hyla miotympanum* differs from *arborescens*, *hazela*, and *charadriicola* by having shorter fingers and toes with more webbing and the anal opening at the upper level of the thighs, instead of at the midlevel of the thighs. *Hyla charadriicola* also differs by having an axillary membrane and by lacking vocal slits. *Hyla hazela* differs by having a yellow venter and a bronze canthal stripe. Other predominantly green Middle American *Hyla* include *Hyla uranochloa*, which has red eyes and a white spot below the eye, and members of the *Hyla eximia* group, which have pointed snouts, less

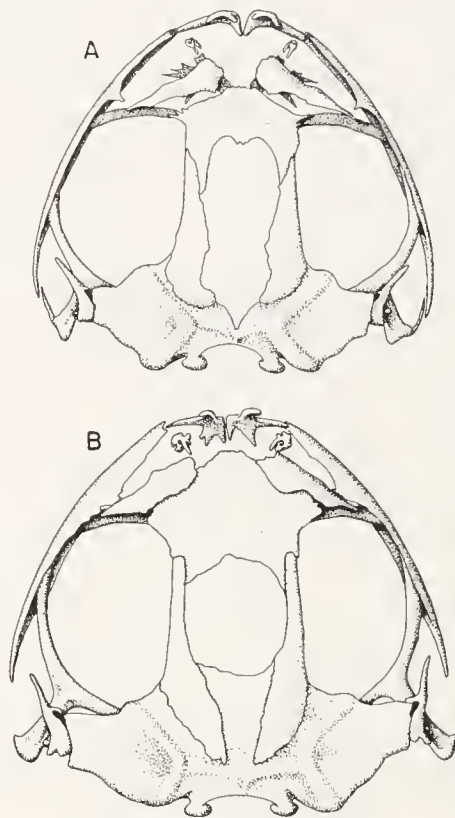


FIG. 182. Dorsal views of the skulls of: A. *Hyla miotympanum*, K.U. No. 59935. B. *Hyla arborescens*, K.U. No. 55605. $\times 5$.

webbing, and usually brown markings on the body and limbs.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 38.4 mm., and females reach 51.0 mm. In a series of 20 males from Barranea Metlae, Veracruz, México, the snout-vent length is 26.8 to 31.1 (mean, 28.5) mm.; the ratio of tibia length to snout-vent length is 0.486 to 0.529 (mean, 0.506); the ratio of foot length to snout-vent length is 0.412 to 0.451 (mean, 0.427); the ratio of head length to snout-vent length is 0.283 to 0.333 (mean, 0.316); the ratio of head width to snout-vent length is 0.297 to 0.325 (mean, 0.315), and the ratio of the diameter of the tympanum to that of the eye is 0.353 to 0.485 (mean, 0.409). Five females from the same locality have snout-vent lengths of 36.8 to 43.6 (mean, 39.7) mm. The females differ from the males by having a slightly larger tympanum; the

ratio of the diameter of the tympanum to that of the eye is 0.462 to 0.579 (mean, 0.519). There is considerable variation in size in various parts of the range. The largest individuals are from the northern part of the range (Nuevo León, Tamaulipas, and San Luis Potosí) and from the southeast, in Chiapas. There are no great differences in proportions, except for the noticeably larger tympanum in individuals from Chiapas (table 37). Throughout the range, females are noticeably larger than males.

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is acutely rounded; in lateral profile, the snout slopes from the nostrils to the margins of the lips. The snout is moderately long; the nostrils are barely protuberant at a point about two-thirds of the distance from the eyes to the tip of the snout. The canthus is angular; the loreal region is barely concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the forelimb. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately short and robust; an axillary membrane is absent. No distinct row of tubercles is present on the ventrolateral edge of the forearm, and the transverse dermal fold on the wrist is indistinct. The fingers are moderately short and bear rather large discs; the width of the disc on the third finger is equal to the diameter of the tympanum. The subarticular tubercles are moderately small and subconical; the distal tubercle on the fourth finger is weakly bifid in some specimens. The supernumerary tubercles are minute and indistinct in many specimens. The palmar tubercle is low, diffuse, and bifid. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about one-third webbed (fig. 183A). The webbing is vestigial between the first and second fingers but extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from the middle of the antepenultimate pha-

lanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the anterior corner of the eye. A transverse dermal fold is present on the heel, and a weak tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, elliptical, and broadly visible from above. The outer metatarsal tubercle is small and conical. The toes are moderately long and robust and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are small and subconical; the supernumerary tubercles are small, but distinct. The toes are about three-fourths webbed (fig. 183C). The webbing extends from the penultimate phalanx of the first toe to the middle of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the upper level of the thighs. A short, broad anal sheath is present, but distinct tubercles are absent below the anal opening. The skin on the dorsal surfaces is smooth; that on the throat, belly, and proximal posteroventral surfaces of the thighs is granular, whereas that on other ventral surfaces is smooth. The tongue is cordiform, shallowly notched behind, and barely free posteriorly. The dentigerous processes of the prevomers are posteromedially inclined elevations between the moderately large, ovoid choanae. Males have two to six (mean, 4.1) teeth on each process, whereas females have four to seven (mean, 5.2) teeth on each process. The vocal slits extend from the posterolateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla miotympanum* consists of a pale green dorsum and a creamy white venter (pl. 56, fig. 1). Usually, when active at night, the frogs are a pale green above with or without small olive-green

TABLE 37
Geographic Variation in Certain Measurements and Proportions
(With Means in Parentheses) of Males of *Hyla miotympanum*

Locality	N	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
Nuevo León: Salto Cola de Caballo	20	30.2-38.4 (33.7)	0.497-0.552 (0.527)	0.392-0.448 (0.427)	0.317-0.347 (0.334)	0.328-0.370 (0.347)	0.405-0.512 (0.461)
Tamaulipas: Sierra de Tamaulipas	3	31.8-34.5 (33.2)	0.503-0.510 (0.507)	0.402-0.423 (0.414)	0.330-0.342 (0.336)	0.336-0.380 (0.358)	0.428-0.526 (0.485)
Tamaulipas: La Joya de Salas	16	31.6-36.2 (33.7)	0.505-0.564 (0.538)	0.438-0.473 (0.454)	0.321-0.357 (0.339)	0.321-0.357 (0.342)	0.418-0.527 (0.465)
San Luis Potosí: Tamazunchale	11	24.6-28.6 (26.9)	0.500-0.533 (0.513)	0.393-0.456 (0.421)	0.323-0.359 (0.338)	0.313-0.351 (0.333)	0.394-0.500 (0.445)
Puebla: Río Totolapa	20	24.5-29.0 (26.7)	0.486-0.557 (0.512)	0.388-0.479 (0.429)	0.305-0.344 (0.326)	0.310-0.354 (0.330)	0.379-0.552 (0.452)
Puebla: Río Octapa	14	25.7-30.7 (27.9)	0.495-0.537 (0.520)	0.408-0.463 (0.435)	0.315-0.350 (0.333)	0.319-0.352 (0.338)	0.382-0.517 (0.467)
Veracruz: Barranca Metlac	20	26.8-31.1 (28.5)	0.486-0.529 (0.506)	0.412-0.451 (0.427)	0.283-0.332 (0.316)	0.297-0.325 (0.315)	0.353-0.485 (0.409)
Veracruz: Cumbres de Acultzingo	13	29.6-34.3 (31.6)	0.492-0.525 (0.509)	0.402-0.453 (0.431)	0.306-0.338 (0.324)	0.319-0.341 (0.331)	0.351-0.486 (0.431)
Veracruz: Los Chaneques	14	28.0-32.9 (30.1)	0.465-0.525 (0.513)	0.385-0.437 (0.417)	0.299-0.348 (0.323)	0.324-0.357 (0.342)	0.333-0.444 (0.422)
Veracruz: Volcán San Martín	20	27.3-33.4 (31.1)	0.476-0.544 (0.508)	0.394-0.459 (0.429)	0.294-0.344 (0.318)	0.309-0.351 (0.326)	0.368-0.486 (0.437)
Chiapas: Rayón Mescalapa	16	32.1-34.7 (33.5)	0.509-0.569 (0.536)	0.377-0.453 (0.422)	0.327-0.355 (0.335)	0.341-0.364 (0.352)	0.447-0.605 (0.508)

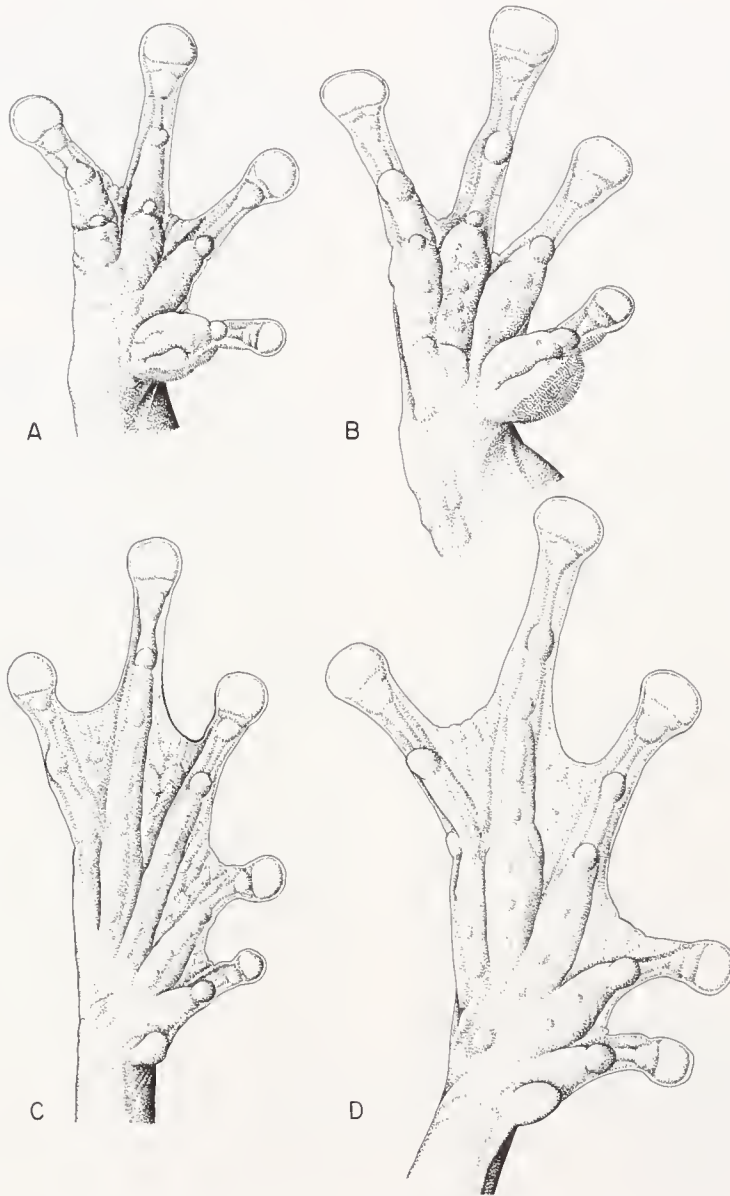


FIG. 183. Hands and feet of members of the *Hyla miotympanum* group. A and C. *Hyla miotympanum*, K.U. No. 57545. B and D. *Hyla arborescens*, K.U. No. 86998. $\times 5$.

flecks. Normally, the flanks are white with black or brown mottling. The belly and chin are white and the ventral surfaces of the limbs and dorsal surfaces of the first and second fingers and toes are pale yellow. The posterior surfaces of the thighs are dull yellowish brown.

Individuals from the northern part of the range have a uniformly pale bronze iris with minute black flecks or reticulations. In specimens from central Veracruz and from the Sierra de los Tuxtlas in southern Veracruz, the upper part of the iris is a deep reddish bronze and the lower part is a pale yellowish

bronze. Specimens from the northern slopes of the Chiapan highlands have a uniformly pale reddish bronze iris.

Throughout the range most individuals have a distinct white transverse stripe above the anal opening and a narrow white or creamy white stripe on the edge of the upper lip, the ventrolateral edge of the forearm, and the outer edge of the foot. The amount of mottling on the flanks is highly variable. In some individuals, there are a few irregular white flecks or spots on the flanks; these spots are separated by lateral extensions of the dorsal ground color. In other individuals the white on the flanks forms a distinct stripe, whereas in other individuals the flanks are pale creamy white with scattered brown or black flecks. The pattern on the flanks does not seem to vary geographically.

Metachrosis is extreme in this species. Although most individuals when active at night are pale green above, some are pale tan with or without fine dark brown or olive-green reticulations. Individuals that are found in bromeliads by day frequently are pale tan with or without darker reticulations on the body. Some individual frogs have been observed to span an exceedingly diverse variety of color permutations. For example, one individual from 3 kilometers southwest of Huatusco, Veracruz, in a matter of three hours changed from a pale green to brown with olive-green reticulations and then to dark

olive-brown with white flecks (pl. 56, figs. 2-4).

TADPOLES: A typical tadpole in developmental stage 33 has a body length of 12.1 mm. and a total length of 35.0 mm. The body is ovoid, only slightly wider than deep. The snout in dorsal profile is bluntly rounded, and in lateral profile, the snout is more acutely rounded. The eyes are moderately small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point slightly closer to the eyes than to the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point slightly below the midline at about midlength of the body. The anal tube is moderately short and dextral. The caudal musculature is moderately heavy and extends nearly to the tip of the rounded tail. At midlength of the tail, the musculature is equal to the depth of the ventral fin and slightly shallower than the depth of the dorsal fin, which does not extend onto the body (fig. 184A).

The body is dark brown, somewhat paler laterally; the venter is bluish gray. The tail is creamy tan with dark brown pigment proximally on the musculature and along the dorsal edge of the musculature nearly to the tip of the tail. Small black flecks are present on the dorsal fin and on the posterior one-third of the ventral fin. In preservative, the body is dark brown; the caudal musculature is creamy tan with a dark brown dorsal edge. The fins

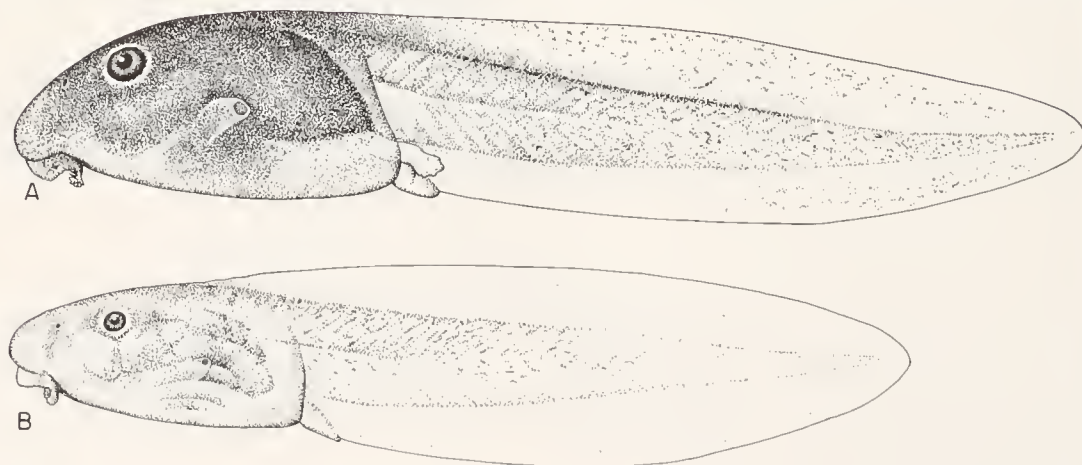


FIG. 184. Tadpoles of members of the *Hyla miotympanum* group. A. *Hyla miotympanum*, K.U. No. 59994. B. *Hyla arborescandens*, K.U. No. 87605. $\times 4$.

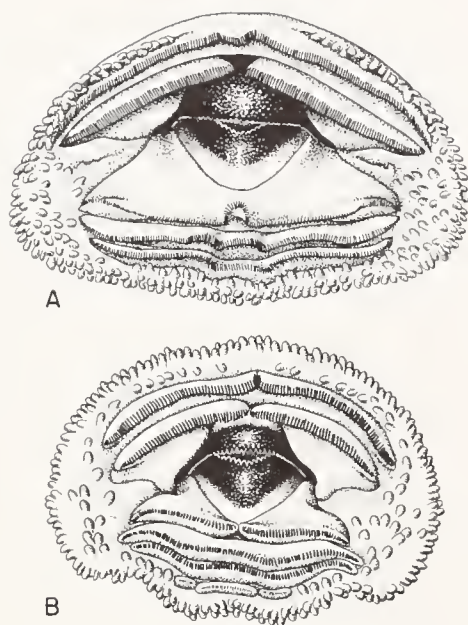


FIG. 185. Mouths of tadpoles of the *Hyla miotympanum* group. A. *Hyla miotympanum*, K.U. No. 59994. B. *Hyla arborescens*, K.U. No. 87605. $\times 15$.

are transparent with scattered small brown flecks.

The mouth is ventral and moderately small; its width is equal to about one-half of the greatest width of the body. Lateral folds are present. The median part of the upper lip is bare, but the rest of the mouth is bordered by a single row of blunt papillae. Additional papillae are present in the lateral folds. The beaks are moderately well developed and bear blunt serrations. The upper beak is in the form of a broad arch with long, slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are equal in length, and the second upper row is narrowly interrupted medially. The three lower rows are approximately the same length, but slightly shorter than the upper rows; the first lower tooth row is interrupted medially in some specimens (fig. 185A).

A developmental series of eggs and tadpoles was obtained on the south slope of Volcán San Martín Tuxtla in southern Veracruz, México. A clump of about 120 eggs was attached to the lee side of a rock in a small stream on August 9, 1960. The eggs

hatched on August 11. The following description of embryonic and larval development is based on that clutch of eggs, tadpoles hatched from those eggs, and tadpoles obtained in the same stream.

The diameter of the eggs, exclusive of membranes, in developmental stage 2 is 2.10 to 2.38 (mean, six eggs, 2.25) mm. The diameter of the fertilization membrane is 3.36 to 5.18 (mean, 4.32) mm., and the diameter of the envelope is 6.3 to 9.8 (mean, 7.70) mm., whereas the diameter of the animal pole is 1.22 to 2.10 (mean, 1.49) mm. In these eggs, the animal pole is dark brown, the gray crescent is clearly visible, and the jelly is clear.

Eggs in developmental stage 3 have a well-defined cleft and are uniformly medium brown. The diameter of five eggs, exclusive of membranes is 2.52 to 2.66 (mean, 2.60) mm.

In 10 eggs in developmental stage 17, the length of the body is 2.87 to 3.47 (mean, 3.18) mm. In most of these embryos the tail bud is well formed. The body is dorsally arched; this is most prominent in the larger embryos. The gill plates are conspicuous but are not divided into visceral arches. The oral suckers are well developed; the optic vesicle is barely visible. The stomodeal cleft is just beginning to invaginate, but there is no indication of proctodeal invagination. The entire egg is uniformly medium to dark brown, except for a paler area on the anteroventral part of the yolk sac.

In 10 hatchlings (developmental stage 19) the body length is 4.8 to 5.1 (mean, 4.92) mm. and the total length is 7.4 to 8.5 (mean, 8.11) mm. In these hatchlings the yolk sac is evident but greatly reduced in size. The gill filaments do not seem to be completely developed. The oral suckers are bifid, and the stomodeal cleft is deeply invaginated. The tail is well developed; the dorsal fin extends almost to the midpoint of the body and is deepest on the posterior one-third of the tail, whereas the ventral fin is deepest anteriorly. The tadpoles are dark brown, but discrete pigment cells are not evident; the cornea and fins are opaque.

Ten tadpoles in developmental stage 25 have body lengths of 7.7 to 9.6 (mean, 8.76)

mm. and total lengths of 19.6 to 26.5 (mean, 23.0) mm. In these tadpoles the mouth is fully developed, although in some individuals the maximum extent of the outer tooth rows has not been attained. The coloration is fully developed, except for pigmentation on the tail.

Five tadpoles in developmental stage 30 have body lengths of 11.5 to 12.7 (mean, 12.2) mm. and total lengths of 30.0 to 36.3 (mean, 33.37) mm. Tadpoles in this stage have fully developed caudal pigmentation consisting of coalesced pigment cells forming venated or branching patterns amidst other discrete cells.

Three tadpoles in developmental stage 42 have body lengths of 12.2 to 12.9 (mean, 12.6) mm. In these tadpoles, the belly and ventral surfaces of the thighs are granular and unpigmented, the digital pads are moderately well developed, and absorption of the tail has begun. The larval mouth parts have been lost, except for some lateral papillae.

Three completely metamorphosed young have snout-vent lengths of 14.1 to 16.7 (mean, 15.2) mm. The dorsum is uniform green and the venter is white.

MATING CALL: The calls of *Hyla miotympanum* are highly variable within and between populations. Recordings were made at four different localities throughout the range (table 38). The call of this species can best be described as a series of moderately short notes that are rather squeaky. Monophasic notes are characteristic of all the samples, except that from Volcán San Martín in southern Veracruz; individuals from there produced biphasic notes. The other principal variables in the calls are the note repetition rate and duration of the notes, which, of course, are correlated. Individuals from Barranca Metlac, Veracruz, consistently produced only one note per call group; these notes had durations of 0.18 to 0.40 (mean, 0.29) of a second and were consistently longer than those produced by frogs at other localities. The dominant frequency, although variable within each sample, is not significantly different between populations. The calls of *Hyla miotympanum* are poorly modulated; consequently, the fundamental fre-

quency cannot be ascertained with any degree of accuracy (pl. 15, fig. 1).

NATURAL HISTORY: Throughout most of its range, *Hyla miotympanum* occurs in cloud forests, where it is active most, if not all, of the year. I have observed mating behavior and heard males calling in every month of the year except October and November, months in which I have not been in the range of *Hyla miotympanum*. Despite the non-seasonal activity of this species, most breeding apparently takes place in the dry season (December through April). At that time of the year, males call along small mountain streams in the cloud forests (pl. 11). The eggs are deposited in the streams, either attached to the lee sides of rocks or to vegetation in the water (fig. 186). During the rainy season, streams that were utilized by *Hyla miotympanum* in the dry season often are roaring torrents, apparently uninhabitable by the adults or tadpoles of this frog. In the rainy season, *Hyla miotympanum* has been observed calling along small seepages and small rivulets, which apparently are much less affected by the rains than are the larger streams.



FIG. 186. Eggs of *Hyla miotympanum*. $\times 2$.

TABLE 38
Geographic Variation in Mating Calls, with Means in Parentheses, in *Hyla miotympanum*.

Sample	N	Structure	Notes per Call Group	Repetition Rate (minite)		Duration (second)		Dominant Frequency (cps)
				Group	Note	Group	Note	
Nuevo León: Salto Cola de Caballo	15	Monophasic	1-3 (2.6)	4-7 (5.2)	45-120 (65)	0.80-0.52 (0.40)	0.02-0.11 (0.04)	2210-2520 (2386)
San Luis Potosí: Tamazunchale	4	Monophasic	1-7 (3.7)	3-6 (4.1)	47-59 (53)	1.2-1.5 (1.2)	0.08-0.22 (0.13)	1750-2825 (2365)
Veracruz: Barranca Metlac ..	3	Monophasic	1	12-21 (17)	12-21 (17)	0.18-0.40 (0.29)	0.18-0.40 (0.29)	2525-2600 (2571)
Veracruz: Volcán San Martín	5	Diphasic	12-46 (27.2)	1-2 (1.3)	58-75 (68)	20.0-40.0 (26.0)	0.16-0.22 (0.19)	1930-2700 (2450)

By day, *Hyla miotympanum* usually is sequestered in bromeliads, or in elephant-ear plants. The frogs have been observed to crawl out of the bromeliads at dusk and down the trees, through bushes, and sometimes onto the ground before reaching their calling sites on low vegetation or rocks along the streams. One individual was observed to utilize the same bromeliad and the same calling site for three consecutive days and nights.

The tadpoles develop in the mountain streams, where they inhabit quiet pools and take refuge amidst detritus on the bottom of the pool or beneath rocks. Some tadpoles have been observed clinging to rocks in the swiftest parts of the streams, but the tadpoles of *Hyla miotympanum* do not appear to be highly adapted for swift water.

REMARKS: Duellman (1964c, p. 455) showed that the type series of *Hyla godmani* Günther was composite; he selected B.M.N.H. No. 1901.12.19.96 from Misantla, Veracruz, as the lectotype of *godmani*. That specimen is the same as the frogs that previously had been referred to as *Hyla rickardsi* Taylor. The other specimens in the type series (B.M.N.H. Nos. 1901.12.19.88-95) are from Jalapa, Veracruz, and are representatives of *Hyla miotympanum*.

Peters (1869, p. 880) named *Hyla microtis* from "Puebla, Mexico." The two syntypes (Z.M.B. No. 6657) are indistinguishable from *Hyla miotympanum*. One individual is a male having a snout-vent length of 34.9 mm., and the other is a female with a snout-vent length of 38.1 mm.

Smith, Smith, and Werler (1952, p. 254) named *Hyla darlingi* from Xico, Veracruz. This specimen is a moderately large (snout-vent length, 40.2 mm.) female of *Hyla miotympanum*; it differs in no morphological characters from females of that species.

The considerable variation in the mating call of *Hyla miotympanum* throughout its range, together with the coloration of the iris, provide a worthwhile problem for investigation. Perhaps, *Hyla miotympanum* as here recognized, is composite; however, on the basis of my own rather extensive field observations and the examination of many preserved specimens, I have been unable to detect the presence of more than one species.

ETYMOLOGY: The specific name, *miotympanum*, is derived from the Greek *meion*, a diminutive prefix and the Greek *tympanon*, meaning drum; the name, meaning a little drum, refers to the small tympanum.

DISTRIBUTION: *Hyla miotympanum* occurs in cloud forests on the Atlantic slopes of the Sierra Madre Oriental at elevations from 100 to 2280 meters from central Nuevo León to central Veracruz, México. Populations also occur on the northern slopes of the Chiapan highlands and in the Sierra de los Tuxtlas in southern Veracruz, where the species descends to an elevation of 370 meters (fig. 187). Three localities are highly questionable. Two specimens from Acapulco, Guerrero (one in F.M.N.H. and one in U.I.M.N.H., both formerly a part of the E.H.T.-H.M.S. collection) supposedly were collected at that locality by Edward H. Taylor. The specimens definitely represent *Hyla miotympanum*, but on the basis of the environment at Acapulco and the extensive collecting done there without revealing the presence of this species, I regard these specimens as having erroneous data. Three specimens in the U.S.N.M. are labeled as having come from Tehuantepec, Oaxaca. These specimens are part of a shipment received from Francis Sumichrast shortly after he had moved to Oaxaca from Mirador, Veracruz, a locality where *Hyla miotympanum* occurs in abundance. The specimens on which Peters based his description of *Hyla microtis* supposedly originated from Puebla, México, and other species in the same collection have been thought to have originated from Izúcar de Matamoros in that state; it is highly unlikely that *Hyla miotympanum* occurs in that arid upper balsas basin in which Izúcar de Matamoros is located.

See Appendix 1 for the locality records of the 1663 specimens examined.

Hyla arborescens Taylor

Hyla arborescens Taylor, 1939a, p. 388 [holotype, U.I.M.N.H. No. 25045 (formerly E.H.T.-H.M.S. No. 3135) from 3 kilometers southwest of Acultzingo, Veracruz, México; Edward H. Taylor and Hobart M. Smith collectors]. Smith and Taylor, 1948, p. 91.

Hyla forbesi Taylor, 1940d, p. 513 [holotype, U.I.M.N.H. No. 25048 (formerly E.H.T.-H.M.S. No. 2276) from 3 miles southwest of Acultzingo, Veracruz,

FIG. 187. Distribution of *Hyla miotympanum*.

México; Dyfrig McH. Forbes collector]. Smith and Taylor, 1948, p. 88.

DIAGNOSIS: This moderate-sized green *Hyla* has the fingers about one-fourth, and the toes about two-thirds, webbed. The anal opening is directed posteroventrally at the

midlevel of the thighs. The species differs from *miotympanum* by having less webbing and by lacking distinct white stripes on the margin of the lips, above the anal opening, and on the outer edges of the forearms and feet. Furthermore, in *miotympanum* the anal

opening is directed posteriorly at the upper level of the thighs. *Hyla hazelae* differs by having much less webbing and a yellow belly. *Hyla arborescendens* resembles certain members of the *Hyla bistincta* group, principally *charadicola*, *robertsororum*, and *siopela*; it differs from all of these by having vocal slits.

DESCRIPTION: Males of this medium-sized species attain a maximum snout-vent length of 37.6 mm., and females reach 51.6 mm. In a series of 23 males from the north slope of the Sierra de Juárez, Oaxaca, México, the snout-vent length is 31.9 to 35.5 (mean, 33.3) mm.; the ratio of tibia length to snout-vent length is 0.472 to 0.520 (mean, 0.495); the ratio of foot length to snout-vent length is 0.432 to 0.486 (mean, 0.454); the ratio of head length to snout-vent length is 0.319 to 0.350 (mean, 0.331); the ratio of head width to snout-vent length is 0.318 to 0.365 (mean, 0.339), and the ratio of the diameter of the tympanum to that of the eye is 0.421 to 0.600 (mean, 0.480). Four females from the same locality have snout-vent lengths of 42.0 to 51.6 (mean, 45.1) mm. Females differ from males by having a proportionately larger tympanum; the ratio of the diameter of the tympanum to that of the eye in females is 0.469 to 0.617 (mean, 0.542). Specimens from farther north have relatively longer legs and feet and smaller tympani. In a series of 18 males from Pan de Olla, Veracruz, the ratio of tibia length to snout-vent length is 0.513 to 0.562 (mean, 0.535); the ratio of foot length to snout-vent length is 0.481 to 0.517 (mean, 0.494), and the ratio of the diameter of the tympanum to that of the eye is 0.357 to 0.500 (mean, 0.425).

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is truncate and posteroventrally inclined. The snout is moderately long; the slightly protuberant nostrils are situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is round, but distinct; the loreal region is barely concave, and the lips are moderately thick and barely flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which other-

wise is distinct and separated from the eye by a distance equal to half again the diameter of the tympanum.

The arms are moderately long; the upper arm is slender, whereas the forearm is moderately robust. An axillary membrane is lacking. A few low tubercles are present on the ventrolateral edge of the forearm, and a weak dermal fold is present on the wrist. The fingers are moderately long and robust and bear large discs; the diameter of the disc on the third finger is slightly greater than the diameter of the tympanum. The subarticular tubercles are large and flat; the distal tubercle on the fourth finger is weakly bifid in some specimens. The supernumerary tubercles are low and indistinct; they are present only on the proximal segments of the digits. A distinct bifid or partially trifid palmar tubercle is present. The prepollex is greatly enlarged and in breeding males bears a spinose nuptial excrescence. The fingers are about one-fourth webbed (fig. 183B). The webbing is vestigial between the first and second fingers, and extends from the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third and on to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately short and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A distinct transverse dermal fold is present on the heel, and a weak tarsal fold extends the full length of the tarsus, but the tarsal fold is evident only distally in many specimens. The inner metatarsal tubercle is low, flat, elliptical, and partly visible from above. The outer metatarsal tubercle is small and subconical. The toes are long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are large and flat and the supernumerary tubercles are low and subconical. The toes are about two-thirds webbed (fig. 183D). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the penultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third,

from the base of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the midlevel of the thighs. A short, narrow anal sheath is present; tubercles are lacking below the anal opening. The skin on the throat, belly, and ventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is cordiform, very shallowly notched posteriorly and not free behind. The denticulous processes of the prevomers are high, narrowly separated, transverse or posteromedially inclined elevations between the large ovoid choanae. Males have four to seven (mean, 5.4) teeth on each process, and females have five to eight (mean, 6.3) teeth on each process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla arborecandens* varies from nearly uniform green above to tan or brown with olive-brown or olive-green mottling or reticulations (pl. 57, figs. 3 and 4). At night the dorsum usually is dull green or olive-green. The belly is white or pale yellow, and the ventral surfaces of the hind limbs are dull yellow. In breeding males, the vocal sac is dull yellow. The posterior surfaces of the thighs are dull yellowish brown. By day, individuals usually are tan or medium brown dorsally; in some specimens, the flanks are pale green. The iris is dull bronze, usually heavily flecked with black. In some specimens, a faint creamy white anal stripe or pair of spots are present; white stripes along the chin and edges of the forearms are absent, but in some individuals a faint pale tan stripe is present on the outer edge of the tarsus. Also, in some individuals a distinct olive-tan or dull bronze colored stripe is present on the canthus and supratympanic fold.

In preservative, the dorsum is dull bluish purple or dull brown with black or dark brown flecks and reticulations. The flanks usually are a paler color, and the ventral surfaces are dull creamy yellow. A few dark flecks are present on the chin in many males. The posterior surfaces of the thighs are dull

brown, and the webbing on the feet is grayish tan.

TADPOLES: A tadpole in developmental stage 25 has a body length of 8.2 mm. and a total length of 28.4 mm. The body is ovoid and only slightly wider than deep. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is round. The eyes are small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed dorsally on the midline at a point about two-thirds of the distance from the snout to the posterior edge of the body. The anal tube is moderately long and dextral. The caudal musculature is moderately robust and it extends nearly to the tip of the rounded tail. The caudal fins are deepest posteriorly and the dorsal fin does not extend onto the body. At midlength of the tail, the depth of the caudal musculature is equal to the depth of the dorsal fin and slightly greater than the depth of the ventral fin (fig. 184B).

In preservative, the body is dull brown, and the caudal musculature is pale creamy tan with dark brown streaks on the proximal dorsal surface. The fins are transparent.

The mouth is ventral and moderately large; its width is equal to about two-thirds the greatest width of the body. Deep lateral folds are present. The mouth is completely bordered by a single row of moderately large, blunt papillae. Additional papillae are present in the lateral folds. The beaks are well developed and bear moderately long, pointed serrations. The upper beak is in the form of a broad arch with long lateral processes. The lower beak is broadly V-shaped. There are two upper and four lower rows of teeth. The two upper rows are long, and the second upper row is narrowly interrupted medially. The lower rows are complete, and the fourth lower row is noticeably shorter than the others, which are only slightly shorter than the upper rows (fig. 185B).

MATING CALL: The call of *Hyla arborecandens* consists of a series of low-pitched, pulsed notes. The duration of each call group varies from 15 to 18 seconds and contains from 16 to 22 notes. The note repetition rate varies

from 64 to 73 notes per minute, and the duration of the notes varies from 0.22 to 0.28 of a second. In one recording, in which the data could be obtained accurately, the pulse rate was 80 pulses per second, the fundamental frequency was 74 cycles per second, and the dominant frequency was 2072 cycles per second (pl. 15, fig. 2).

NATURAL HISTORY: *Hyla arborescendens* inhabits cloud forests and cool montane pine-oak forests, where the species lives in the immediate vicinity of small streams. Males have been heard to call throughout most of the year, and the breeding season in this species probably is lengthy. Although some individuals can be found on rocks in and along, or vegetation over, streams by day, the usual day-time retreat of *Hyla arborescendens* is in bromeliads growing on trees near the streams.

Tadpoles have been found in quiet pools in rocky streams. When disturbed, they seek refuge beneath rocks or in the detritus at the bottom of the pool.

REMARKS: Examination of the holotype of *Hyla forbesi* Taylor (U.I.M.N.H. No. 25048) reveals that this specimen is nothing more than a female of *Hyla arborescendens*. The large females of this species are easily confused with members of the *Hyla bistincta*

group, especially *Hyla robertsoni* and *siopepla*.

Hyla hazelae is easily confused with *Hyla arborescendens*, especially on the basis of preserved specimens. The former has a proportionately larger head and a distinct canthal stripe. The major differences between the two species are evident in the cranial osteology and in the mating calls (see account of *Hyla hazelae*).

ETYMOLOGY: The specific name is derived from the Latin *arbor*, meaning tree, and the genitive of the Latin *scando*, meaning to climb; literally, the name means a climber of trees.

DISTRIBUTION: *Hyla arborescendens* occurs in cloud forests and pine-oak forests at elevations of 1600 to 3100 meters in the Sierra Madre Oriental from northern Puebla to central Oaxaca, México (fig. 188).

See Appendix 1 for the locality records of the 198 specimens examined.

The *Hyla hazelae* Group

DEFINITION: The members of this group are small, stream-breeding species; males attain a maximum snout-vent length of 38.6 mm., and females reach 37.8 mm. (females of largest species unknown). The dorsum is uniform green or mottled green and brown, and the venter is pale yellow or white with bold mottling. The palpebral membrane is clear. The webbing on the hand is vestigial, and the feet are only about one-half webbed. Dermal fringes and appendages are lacking on the limbs, and an axillary membrane is absent. The tympanum is distinct and about one-half of the size of the eye. Males have nuptial excrescences, vocal slits, and a single, large, median, subgular vocal sac. The cranial elements are moderately well ossified. An ovoid frontoparietal fontanelle exists between the moderately developed frontoparietals (fig. 189). The sphenethmoid is large, truncate, or notched anteriorly, and extends far anteriorly between the large nasals. The nasals are separated medially and in bony contact with the sphenethmoid (*hazelae*) or not (*thorectes*). The quadratojugal is reduced to a small spur or is absent; the squamosal is not in bony contact with the crista parotica, and the anterior arm of the maxillary extends only

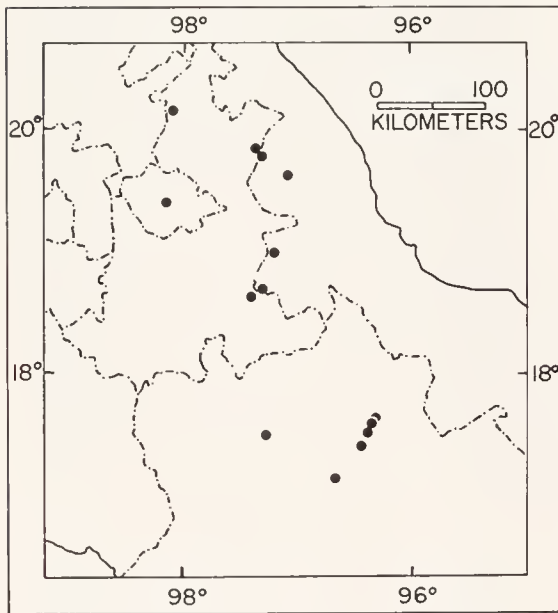


FIG. 188. Distribution of *Hyla arborescendens*.

about one-half of the distance to the maxillary. The medial ramus of the pterygoid does not have a bony articulation with the prootic. Prevomerine teeth are present. The known tadpoles have small ventral mouths, completely bordered by papillae and bearing two upper and three lower rows of teeth. The calls consist of short moderately low-pitched notes that are produced singly or in pairs. The number of chromosomes is unknown.

COMPOSITION: Two species (*Hyla hazelae* and *thorectes*) comprise this group, which is endemic to the mountains of Oaxaca, México. Forty-one preserved frogs, two skeletons, three lots of tadpoles, and three preserved clutches of eggs have been examined.

COMMENTS: The two species placed in this group are noticeably different in coloration but possess certain common external and osteological characters that distinguish them from other Middle American hylids. The combination of large hands with vestigial webbing, half-webbed feet (fig. 190), and presence of a tympanum are external features which separate these species from other small stream-breeding Mexican *Hyla*. Furthermore, both species have small, relatively narrow tongues and large tubercles below the anal opening. The nature of the nasals and sphenethmoid are unique among the northern Middle American hylids.

Members of this group seem to be somewhat intermediate between *Hyla arborescan-*

dens and members of the *Hyla bistincta* group. *Hyla hazelae* and *thorectes* apparently differentiated from one another through isolation by the xeric Valley of Oaxaca; the former occurs on Cerro San Felipe north of the valley, and the latter inhabits cloud forests on the southern slopes of the Sierra Madre del Sur south of the valley.

Hyla hazelae Taylor

Hyla hazelae Taylor, 1940c, p. 385 [holotype, F.M.N.H. No. 100047 (formerly E.H.T.-H.M.S. No. 16262) from Cerro San Felipe, 15 kilometers northeast of Oaxaca, Oaxaca, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 90.

DIAGNOSIS: This moderately small, stream-breeding species has a green dorsum, pale yellow belly, and a bronze canthal stripe. It can be distinguished from all other green Middle American *Hyla* by having vestigial webbing on the hand and the feet only about half webbed. It differs from *thorectes* by lacking a mottled dorsum and heavily blotched throat and belly. *Hyla uranochroa* and *Ptychohyla schmidtorum chamulae* are the only other Middle American hylids resembling *hazelae* in coloration; both differ by having a white spot below the eye and by having more webbing.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 38.6 mm.; females are unknown. In a series of seven males from Cerro San Felipe, Oaxaca, México, the snout-vent length is 35.0 to 38.6 (mean, 36.8) mm.; the ratio of tibia length to snout-vent length is 0.461 to 0.494 (mean, 0.480); the ratio of foot length to snout-vent length is 0.407 to 0.457 (mean, 0.440); the ratio of head length to snout-vent length is 0.304 to 0.327 (mean, 0.312); the ratio of head width to snout-vent length is 0.325 to 0.340 (mean, 0.331), and the ratio of the diameter of the tympanum to that of the eye is 0.419 to 0.587 (mean, 0.472).

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded, and in lateral profile it is round. The snout is moderately short, and the nostrils are barely protuberant at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is barely



FIG. 189. Dorsal view of the skull of *Hyla hazelae*, K.U. No. 100968. $\times 5$.

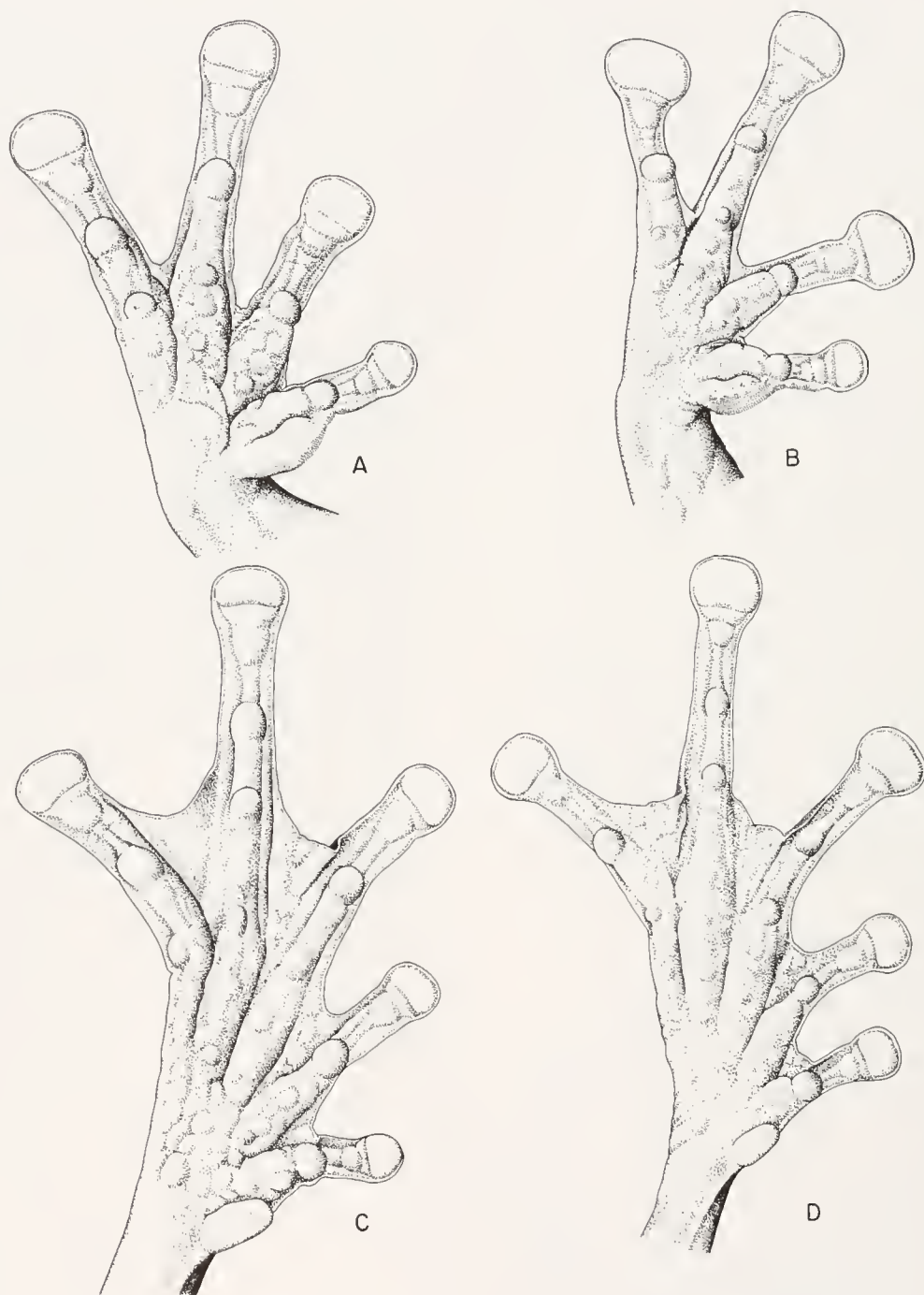


FIG. 190. Hands and feet of members of the *Hyla hazelae* group. A and C. *Hyla hazelae*, K.U. No. 100969. B and D. *Hyla thorectes*, K.U. No. 100951. $\times 5$.

concave, and the lips are thick and barely flared. A heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is only barely distinct. The tympanum is separated from the eye by a distance equal to twice the length of the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. A row of low tubercles is present on the ventrolateral edge of the forearm, and a distinct dermal fold is present on the wrist. The fingers are moderately long and slender and bear medium-sized discs; the width of the disc on the third finger is slightly greater than the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; none is bifid. The supernumerary tubercles are large and subconical. A large, triangular palmar tubercle is present. The prepollex is greatly enlarged and in breeding males bears a nuptial excrecence. The fingers are barely webbed (fig. 190A). The legs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A weak tarsal fold is evident on the posterior half of the tarsus. The inner metatarsal tubercle is elongately elliptical, flat, and visible from above. An outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are somewhat smaller than those on the fingers. The subarticular tubercles are moderately large and subconical; the supernumerary tubercles are large and distinct. The toes are about one-half webbed (fig. 190C). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the base of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs. A distinct

anal sheath is present. A large tubercle and several smaller tubercles are present ventrally on each side of the anal opening. The skin of the dorsum and ventral surfaces of the arms and legs, except thighs, is smooth; that on the throat, belly, and ventral surfaces of the thighs is strongly granular. The tongue is elongately elliptical, emarginate posteriorly, and barely free behind. The dentigerous processes of the prevomers are large, posteromedially inclined elevations between the moderately small, ovoid choanae. There are four or five teeth on each process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is large, median, single, and subgular.

The general coloration of *Hyla hazelae* is green above and pale yellow below (pl. 57, fig. 1). The dorsum is dark green with pale green flecks. Distinct dull bronze stripes are present on the upper lip, the edge of the canthus, and on the supratympanic fold. The flanks are mottled dark brown and creamy white. The anterior and posterior surfaces of the thighs vary from purplish brown to orange-brown. The anal stripe and anal tubercles are white. The belly is creamy yellow; the distended vocal sac is pale yellow, whereas when collapsed it is greenish tan with yellow flecks. The iris is deep bronze with black reticulations.

In preservative, the dorsum varies from purplish brown to dull bluish gray, usually distinctly marked with pale bluish white flecks. The flanks are dull brown with creamy white flecks and reticulations, and the venter is creamy yellow. The labial, canthal, and supratympanic stripes are dull brown in freshly preserved specimens, whereas in older specimens, these stripes are not evident. The anal stripe and anal tubercles are white in all specimens.

TADPOLES: The tadpoles of this species are unknown.

MATING CALL: Two recordings of this species are available. The call consists of individual notes or short groups of notes repeated quickly. One individual produced 23 notes in one minute. One or two notes were produced most frequently in this series of notes, but the frog produced one set of three and one set of four notes. Another individual pro-

duced 28 notes in one minute with one or two notes in each group; groups of two were most common. The duration of each note varies from 0.5 to 0.7 of a second, and the pulse rate varies from 120 to 140 pulses per second. The dominant frequency varies from 1800 to 1850 cycles per second (pl. 16, fig. 2).

NATURAL HISTORY: Taylor (1940c, p. 385) found individuals of this species along a small stream on Cerro San Felipe, Oaxaca. In August, 1966, I found individuals calling from bushes over and near small streams in pine-oak forests on the slopes of Cerro San Felipe.

REMARKS: It is possible that some of the specimens referred to *Hyla arborescendens*, that were collected on Cerro San Felipe, actually are *Hyla hazelae*. Most of these specimens are sufficiently darkened by preservative, that the diagnostic stripes cannot be ascertained.

ETYMOLOGY: The specific name is a patronym for Mrs. Hazel Roberts, who aided Edward H. Taylor in collecting amphibians and reptiles on Cerro San Felipe.

DISTRIBUTION: *Hyla hazelae* is known only from elevations in excess of 2300 meters on Cerro San Felipe and Cerro Machín in central Oaxaca, México (fig. 191).⁹

See Appendix 1 for the locality records of the 19 specimens examined.

Hyla thorectes Adler

Hyla thorectes Adler, 1965, p. 10 [holotype, U.M.M.Z. No. 124390 from 37 kilometers north (by road) of San Gabriel Mixtepec, Oaxaca, México, elevation 1860 meters; Kraig Adler collector].

DIAGNOSIS: This moderately small species has a mottled brown and green dorsum, throat and chest boldly mottled with dark brown or black, fingers essentially lacking webs, and feet only about half webbed. The mottling on the venter immediately distinguishes *Hyla thorectes* from all other Middle American hylids.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent

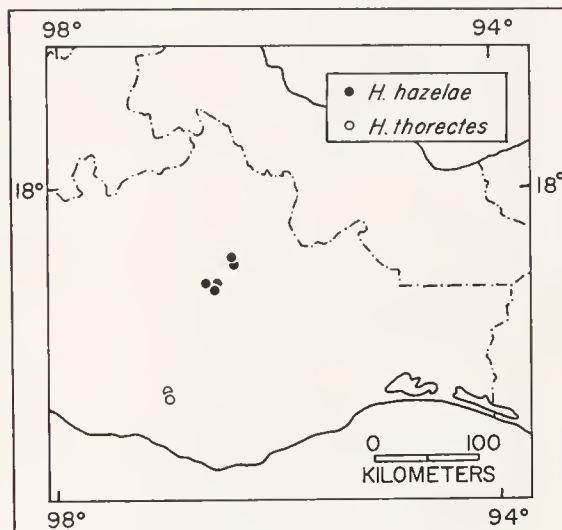


FIG. 191. Distribution of *Hyla hazelae* and *Hyla thorectes*.

length of 34.2 mm., and females reach 37.3 mm. In a series of 20 males from the south slope of the Sierra Madre del Sur, 37 kilometers north of San Gabriel Mixtepec, Oaxaca, México, the snout-vent length is 29.8 to 34.2 (mean, 31.9) mm.; the ratio of tibia length to snout-vent length is 0.485 to 0.511 (mean, 0.496); the ratio of foot length to snout-vent length is 0.438 to 0.482 (mean, 0.464); the ratio of head length to snout-vent length is 0.300 to 0.330 (mean, 0.310); the ratio of head width to snout-vent length is 0.316 to 0.357 (mean, 0.337), and the ratio of the diameter of the tympanum to that of the eye is 0.342 to 0.412 (mean, 0.385). One female from the same locality has a snout-vent length of 37.3 mm. and differs from males in having a proportionately larger tympanum. The ratio of the diameter of the tympanum to that of the eye is 0.500.

The head is as wide as, or slightly wider than, the body, and the top of the head is flat or barely convex. In dorsal profile, the snout is bluntly rounded with a minute point terminally; in lateral profile, the snout is truncate, barely rounded dorsally. The snout is short, and the noticeably protuberant nostrils are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is moderately angular, and the loreal region is barely concave; the lips are

⁹ Dr. Robert G. Webb recently obtained two specimens of a frog that probably is this species. The specimens were collected on July 21, 1968, at 16 kilometers southwest of Cuquila, Oaxaca, elevation 2400 meters. This locality is just north of Chichahuaxtla on the road to Putla in the Sierra Madre del Sur.

thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct. The tympanum is separated from the eye by a distance equal to nearly twice the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane is absent. A low, scalloped dermal fold, composed of interconnected tubercles is present on the ventrolateral surface of the forearm; a distinct dermal fold is present on the wrist. The fingers are moderately long and slender and bear large discs; the width of the disc on the third finger is nearly twice the diameter of the tympanum. The subarticular tubercles are moderately large and subconical; none is definitely bifid. The supernumerary tubercles are small and conical. A large, flat, partially bifid palmar tubercle is present. The prepollex is moderately enlarged and bears nuptial excrescences in breeding males. The fingers are barely webbed (fig. 190B). The legs are moderately short and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the posterior corner of the eye. A distinct transverse dermal fold is present on the heel, and a low tarsal fold is present on the posterior two-thirds of the tarsus. The inner metatarsal tubercle is small, elliptical, and visible from above. A minute outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately small and subconical; the supernumerary tubercles are minute and indistinct. The toes are about one-half webbed (fig. 190D). The webbing extends from the base of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the base of the antepenultimate phalanx of the fourth, and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs. A moderately long anal sheath is present, and numerous small tubercles are present below the anal opening. The skin on the throat, belly, and posteroventral surfaces of the thighs is granular, whereas that on the other surfaces is smooth. The tongue is elongately ovoid, emarginate or shallowly notched posteriorly, and barely free behind. The denticulous processes of the prevomers are widely separated, transverse or posteromedially inclined elevations between the small, round choanae. Males have three to six teeth on each process, whereas females have five to eight teeth on each process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla thorectes* is mottled dark brown and green above and white with brown or black mottling below (pl. 57, fig. 2). The dorsum is usually reddish tan with dark brown flecks and metallic green flecks. The same color is present on the dorsal surfaces of the forelimbs, shanks, and feet. The dorsal surfaces of the thighs are brown with creamy tan mottling. The anterior and posterior surfaces of the thighs are dull tan. The upper flanks and axilla are pale yellow, whereas the lower flanks are white. The flanks are mottled with black. The throat and belly are white with dark gray or dark brown mottling or spots. The ventral surfaces of the limbs are dull yellow. The anal spots are creamy white, and the webbing on the feet is dull brown. The iris is dull bronze and heavily reticulated with black.

One individual was pale yellowish tan above with many small dark brown flecks and a few metallic green spots. By day, the dorsum becomes a darker brown, reddish brown in some individuals. The mottling on the ventral surfaces is black by day.

In preservative, the dorsum is dull brown with faint bluish gray flecks or spots. The flanks are creamy white with brown or black mottling, and the anterior and posterior surfaces of the thighs are dull brown. Distinct transverse anal stripe and spots are present. The venter is creamy tan with dark brown or

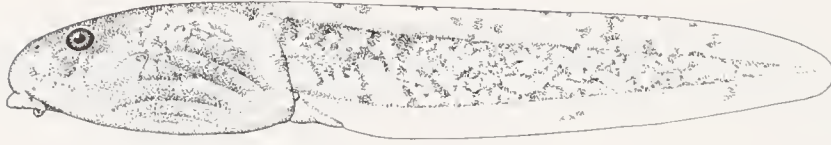


FIG. 192. Tadpole of *Hyla thorectes*, K.U. No. 104169. $\times 3$.

black spots and mottling on the throat and anterior part of the belly.

TADPOLES: A typical tadpole in developmental stage 27 has a body length of 11.4 mm. and a total length of 34.8 mm. The body is elongately ovoid and not depressed. In dorsal profile, the snout is bluntly rounded, and in lateral profile, it is round. The eyes are moderately small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is on the midline at a point about midway of the length of the body. The anal tube is long and dextral. The caudal musculature is robust and extends nearly to the tip of the long, terminally rounded tail. At midlength of the tail, the depth of the caudal musculature is equal to the combined depths of the dorsal and ventral fins. The dorsal fin does not extend onto the body (fig. 192).

The body is dark brown with bluish white flecks on the flanks and silvery flecks on the belly. The caudal musculature is tan with brown flecks and the iris is pale gold. In preservative, the body is dull brown, and the caudal musculature is creamy tan with dull brown flecks. A few flecks are present on the transparent fins.

The mouth is ventral and small; its width is equal to somewhat less than half of the greatest width of the body. The mouth is completely bordered by a single row of small, blunt papillae. The lips are indented laterally; in this lateral fold, additional papillae are present. The beaks are moderately robust and bear large pointed serrations. The upper beak forms a broad arch with long slender lateral processes; the lower beak is broadly V-shaped. There are two upper and three lower rows of teeth. The upper rows are nearly equal in length; the second upper row is narrowly interrupted medially. The lower rows are complete; the first and second

lower rows are nearly as long as the upper ones, but the third lower row is noticeably shorter (fig. 193).

Hatchlings are in developmental stage 25, except that the spiracle is not apparent. The hatchling tadpoles lack gills and have no yolk bulge, but a faint amount of yolk is present in the gut. The eye is well developed. These small tadpoles are good swimmers and have two upper and three lower rows of teeth upon hatching. All of the teeth are slightly irregular, and the third lower row is poorly developed. The upper beak is keratinized but not the lower one. Fringing papillae are present in the same state as in tadpoles of much greater age. Two hatchlings have body lengths of 4.0 and 4.1 mm. and total lengths of 14.2 and 14.9 mm. Five tadpoles that were preserved at an age of 21 days are still in developmental stage 25; these individuals have a well-developed spiracle and completely developed caudal pigmentation. In these specimens, the body length varies from 5.0 to 5.5 mm., and the total length varies from 15.0 to 16.8 mm.

MATING CALL: The call consists of a series of moderately low-pitched notes. Call groups are composed of six to 24 notes, and the interval between call groups varies from 1.5 to more than five minutes. The note repetition

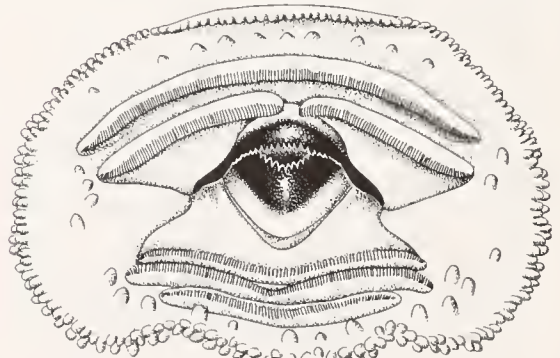


FIG. 193. Mouth of tadpole of *Hyla thorectes*, K.U. No. 104169. $\times 20$.

rate is approximately 24 notes per minute. The notes have a duration of 0.17 to 0.25 (mean, 0.21) of a second and a pulse rate of 60 to 70 (mean, 67) pulses per second. The fundamental frequency varies from 122 to 134 (mean, 126) cycles per second, and the dominant frequency varies from 2010 to 2108 (mean, 2062) cycles per second (pl. 16, fig. 1).

Males usually call in pairs; one individual answers the other almost immediately.

NATURAL HISTORY: Adler (1965, p. 13) noted that he found this species calling from low vegetation along a stream on June 23. In August, 1966, I obtained males calling from herbs, bushes, ferns, and low trees over streams at night. Some males and females were sitting on trees near, but not over the stream.

Tadpoles in later developmental stages were obtained from streams in February. The tadpoles cling to rocks in quiet pools; when they are disturbed they seek refuge in the mud or leaf litter at the bottom of the pool.

Hyla thorectes is unique among members of the genus in northern Middle America by depositing its eggs on vegetation above the stream. Three clutches of 10 eggs each were found on the tips of leaves or the tips of the fronds of ferns. The large eggs have a diameter of about 5.1 mm.; the diameter of the developing embryo is about 4.2 mm.

One recently metamorphosed young having a snout-vent length of 18.2 mm. was found on a bush at the edge of a stream in August. The dorsum was bronze-tan with metallic green flecks. The anterior and posterior surfaces of the thighs and the hands and feet were yellow.

REMARKS: Although *Hyla thorectes* differs significantly from *hazelae* in coloration, the two are somewhat alike in their external structural features and in the nature of the sphenethmoid and the nasal. Consequently, they are placed together in one group.

ETYMOLOGY: The specific name is Greek, meaning a warrior armed with a breast-plate and refers to the boldly marked chest and throat.

DISTRIBUTION: *Hyla thorectes* is known only from elevations between 1600 and 1900 meters on the Pacific slopes of the Sierra

Madre del Sur in Oaxaca, México (fig. 191).

See Appendix 1 for the locality records of the 30 specimens examined.

The *Hyla erythromma* Group

DEFINITION: Frogs in this group belong to a moderately small, stream-breeding species; males attain a maximum snout-vent length of 36.3 mm., and females, 57.6 mm. The dorsum is pale green with no markings other than small dark brown or black flecks; there are no transverse bands on the limbs, and the posterior surfaces of the thighs are dull yellowish tan, but white stripes are present on the outer edges of the forearms and feet. The palpebral membrane is reticulated, and the iris is red. The fingers are about one-fourth webbed, and the toes are two-thirds webbed. Dermal fringes and appendages are absent from the limbs. A tarsal fold and an abbreviated axillary membrane are present. Males have a single, median, subgular vocal sac and bony nuptial excrescences on the polices. The cranial elements are moderately well ossified; a large frontoparietal fontanelle is present. The sphenethmoid is short and does not extend anteriorly between the nasals, which are broadly separated medially and not in contact with the sphenethmoid (fig. 194). The quadratojugal is present. The squamosal is in bony contact with the crista parotica, and the anterior arm of the squamosal extends about half the distance to the

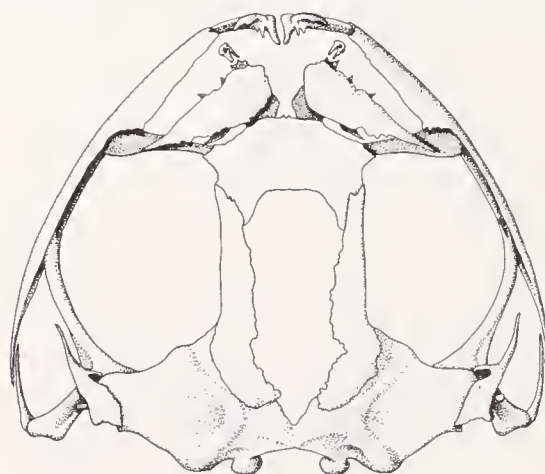


FIG. 194. Dorsal view of the skull of *Hyla erythromma*, K.U. No. 87782. $\times 6$.

maxillary. The medial ramus of the pterygoid is not in bony contact with the prootic. Prevomerine teeth are present. The tadpoles have moderately long tails and medium-sized ventral mouths with four upper and six lower rows of teeth. The mating call consists of a single, long, moderately low-pitched, slowly pulsed note. The haploid number of chromosomes is 12.

COMPOSITION: One species (*Hyla erythromma*) is included in the group, which inhabits moderate elevations in southern México. Seventy-eight preserved frogs, two skeletons, seven lots of tadpoles, and one preserved clutch of eggs have been examined.

COMMENTS: Superficially, *Hyla erythromma* resembles *Hyla miotympanum* in structure, coloration, and in the great sexual dimorphism in size. However, *erythromma* has a quadratojugal and tadpoles with four upper and six lower rows of teeth, whereas *miotympanum* lacks a quadratojugal and has tadpoles with two upper and three lower rows of teeth. On the basis of these differences, *erythromma* is placed in a group apart from *miotympanum*. It is most likely that the two groups evolved from a common ancestral stock that had a quadratojugal and tadpoles with two upper and three lower rows of teeth. The members of the *Hyla miotympanum* phyletic line (*arborescendens* and *miotympanum*) lost the quadratojugal and retained a generalized tadpole, whereas *erythromma* retained the quadratojugal and developed specialized tadpoles.

Hyla erythromma Taylor

Hyla erythromma Taylor, 1937, p. 48 [holotype, F.M.N.H. No. 100083 (formerly E.H.T.-H.M.S. No. 5976) from Agua del Obispo, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 89.

DIAGNOSIS: This moderately small green frog is immediately distinguished from all other Mexican *Hyla* by having a red iris and a faintly reticulated palpebral membrane. In preservative, it is very similar to *Hyla miotympanum*, which differs by having more webbing between the fingers and a less distinctive white stripe on the outer edge of the foot. *Hyla erythromma* has an abbreviated axillary membrane and white flecks postero-

lateral to the anal opening; both of these are absent in *miotympanum*. Other red-eyed Middle American hylids include several species of *Agalychnis*, which have vertical pupils, and members of the *Hyla uranochroa* group; the latter have short, truncate snouts, and *Hyla uranochroa*, the green species in the group, has a large white spot below the eye.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 36.3 mm. and females reach 57.6 mm. In a series of 25 males from 8 kilometers south of Yctla, Oaxaca, México, the snout-vent length is 30.5 to 36.3 (mean, 33.2) mm.; the ratio of tibia length to snout-vent length is 0.517 to 0.579 (mean, 0.546); the ratio of foot length to snout-vent length is 0.378 to 0.458 (mean, 0.416); the ratio of head length to snout-vent length is 0.335 to 0.361 (mean, 0.347); the ratio of head width to snout-vent length is 0.329 to 0.354 (mean, 0.341), and the ratio of the diameter of the tympanum to that of the eye is 0.476 to 0.560 (mean, 0.520). Four females from the same locality have snout-vent lengths of 45.0 to 57.6 (mean, 50.6) mm. and do not differ significantly from the males in any proportions.

The head is as wide as the body, and the top of the head is flat; the eyes are large and protuberant. In dorsal profile the snout is acutely rounded, and in lateral profile it is bluntly rounded. The snout is moderately long; the nostrils are noticeably protuberant with a depressed internarial region and are situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is angular and distinctly curved; the loreal region is barely concave, and the lips are moderately thick and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to the point of insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to the diameter of the tympanum.

The arms are moderately long and slender; a short axillary membrane extends about one-fourth of the length of the upper arm. A row of distinct tubercles is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist.

The fingers are moderately long and robust and bear large discs; the width of the disc on the third finger is equal to the diameter of the eye. The subarticular tubercles are moderately large and subconical; the distal tubercle on the fourth finger is distinctly bifid in most specimens. The supernumerary tubercles are small and subconical. A low, flat, bifid palmar tubercle is present. The prepollex is moderately enlarged and in breeding males, bears a horny nuptial excrescence. The fingers are about one-fourth webbed (fig. 195A). The webbing is vestigial between the first and second fingers, but connects the second finger from the base of the penultimate phalanx to the base of the antepenultimate phalanx of the third, and from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the snout. A transverse dermal fold and a conical tubercle are present on the heel. A thin, tarsal fold extends the full length of the tarsus; in some individuals this fold is barely discernible. The inner metatarsal tubercle is elongate, flat, and barely visible from above. A distinct, conical, outer metatarsal tubercle is present. The toes are moderately long and slender and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are moderately small and subconical, and the supernumerary tubercles are distinct and subconical. The toes are about two-thirds webbed (fig. 195B). The webbing extends from the distal end of the penultimate phalanx of the first toe to the distal end of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third, from the base of the disc of the third to the middle of the antepenultimate phalanx of the fourth, and from the distal end of the antepenultimate phalanx of the fourth to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the upper level of the thighs. A broad anal sheath is present and numerous tubercles

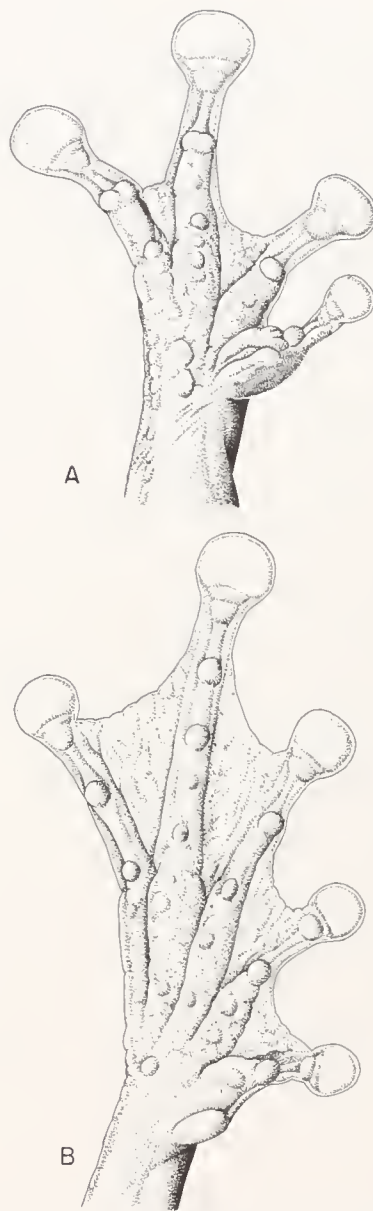


FIG. 195. Hand (A) and foot (B) of *Hyla erythromma*, K.U. No. 87089. $\times 5$.

are present below and lateral to the anal opening. The skin on the throat, belly, and proximal posteroventral surfaces of the thighs is granular; elsewhere, the skin is smooth. The tongue is cordiform or elongately ovoid and not free behind. The dentigerous processes of the prevomers are small, widely separated, transverse or posteromedially in-

elined ridges between the moderately large, ovoid choanae. Males have four to seven (mean, 5.1) and females have seven to nine (mean, 8.1) teeth on each process. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla erythromma* is green above and white below with a distinctive red iris (pl. 56, fig. 5). When active at night, the dorsum is dark green with pale green flecks in some individuals. Creamy white stripes are present on the edge of the upper lip, the length of the flanks, and on the outer edges of the forearm and tarsus. The anal tubercles and anal stripe are white. The anterior surfaces of the thighs are orange-tan, and the posterior surfaces are orange-brown. The chin and chest are white, and the belly is pale creamy yellow. The under-surfaces of the legs are yellowish tan, and the ventral surfaces of the feet are brown. The webbing is tan. The iris is bright red and the palpebral membrane is faintly reticulated with greenish gold.

In preservative the dorsum is pale grayish tan or bluish gray with or without darker flecks. The anterior and posterior surfaces of the thighs are yellowish brown, and the venter is creamy white. In males, the venter is usually unmarked, whereas in females, brown flecks are present on the chest and on the edge of the chin. The flanks are brown with heavy white flecking. The edge of the upper lip, the outer edges of the forearms and feet, and the anal stripe are white. In specimens that have been preserved from three to five years, the iris is pale reddish bronze or pale yellow.

TADPOLES: One tadpole in developmental stage 25 has a body length of 9.5 mm. Three tadpoles in developmental stage 38 have body lengths of 12.5 to 13.0 (mean, 12.8) mm. and

total lengths of 37.5 to 40.0 (mean, 38.5) mm. Eight tadpoles in developmental stage 41 have body lengths of 13.0 to 14.0 (mean, 13.6) mm. and total lengths of 37.5 to 41.5 (mean, 40.1) mm. Two tadpoles in developmental stage 43 each have a body length of 14.5 mm.

A typical tadpole in developmental stage 38 has a body length of 13.0 mm. and a total length of 40.0 mm. The body is rather robust and nearly as deep as wide. In dorsal profile, the snout is bluntly rounded and in lateral profile is is acutely rounded. The eyes are moderately small, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about two-fifths of the distance from the eyes to the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point below the midline and about three-fifths of the distance from the snout to the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is robust and tapers gradually to a point just short of the terminally acute caudal fin. At midlength of the tail, the depth of the caudal musculature is noticeably greater than that of either the dorsal or ventral fin. The dorsal fin does not extend onto the body (fig. 196).

The body and the dorsal part of the caudal musculature anteriorly is pale brown. The lateral surfaces of the caudal musculature are heavily flecked with dark brown, and dark brown flecks are present on the otherwise transparent caudal fin. The iris is red. In preservative, the body is dull brown; this color extends posteriorly on the dorsal surfaces of the tail, which is distinctly demarked laterally by dark brown. The ventral fin has a few dark brown flecks posteriorly, whereas flecks and small blotches are present throughout the length of the dorsal fin.

The mouth is moderately large and ventral; the lips are broadly indented laterally. There are at least two rows of small papillae

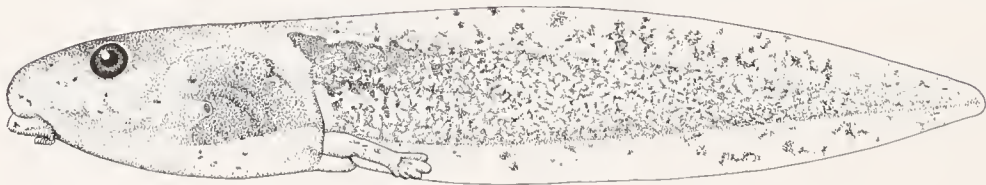


FIG. 196. Tadpole of *Hyla erythromma*, K.U. No. 87630. $\times 3$.

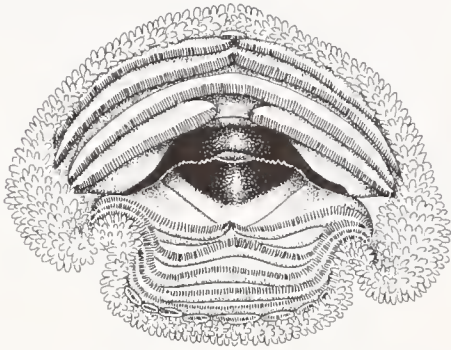


FIG. 197. Mouth of tadpole of *Hyla erythromma*, K.U. No. 87630. $\times 17$.

completely bordering the mouth; three or more rows are present on parts of the lower lip in some specimens, and additional small papillae are present in the lateral fold. The beaks are slender and bear blunt serrations. The upper beak is in the form of a broad arch with slender, terminally expanded lateral processes. The lower beak is shallowly V-shaped. There are four upper and six lower rows of teeth. The upper rows are about equal in length and extend to the edges of the lips; the fourth upper row is narrowly interrupted medially. The lower rows are complete; the first four or five lower rows are nearly as long as the upper rows, but the fifth and sixth usually are noticeably shorter (fig. 197).

MATING CALL: The call of *Hyla erythromma* consists of a long, moderately low-pitched, slowly pulsed note. Each call group consists of a single note, and call groups are repeated at intervals of about 30 to 50 seconds. In one analyzable recording (pl. 15, fig. 3) the note has a duration of 0.62 of a second, 26 pulses per second, a fundamental frequency of 87 cycles per second, and a dominant frequency of 2266 cycles per second.

NATURAL HISTORY: *Hyla erythromma* inhabits the lower reaches of montane cloud forests and low pine-oak forests. In streams in northern Oaxaca, numerous individuals have been found at night on vegetation along the streams in the rainy season; noticeably fewer individuals have been observed along the same streams in the dry season, although males have been heard to call at both times of the year. Tadpoles have been found in the

streams in June, July, and February. The tadpoles inhabit quiet pools in the streams and seek shelter amidst debris in the bottom of the stream.

Metamorphosing young have been found in Oaxaca and in Guerrero in June. The young have the bright red iris of the adults and are distinctly marked with white elbows and heels and a white labial stripe, all of which contrast with the dull olive-green dorsum.

REMARKS: I have not seen living or recently preserved adults from Guerrero. Some minor differences exist between the old preserved specimens from Guerrero and the fresh material from Oaxaca. The specimens from Guerrero tend to be more slender and have narrower digits on the finger. The differences in these highly subjective characters most likely are due to differential preservation. I am unable to find differences in the tadpoles from Guerrero from those from Oaxaca, and recently metamorphosed young from the two regions are identical.

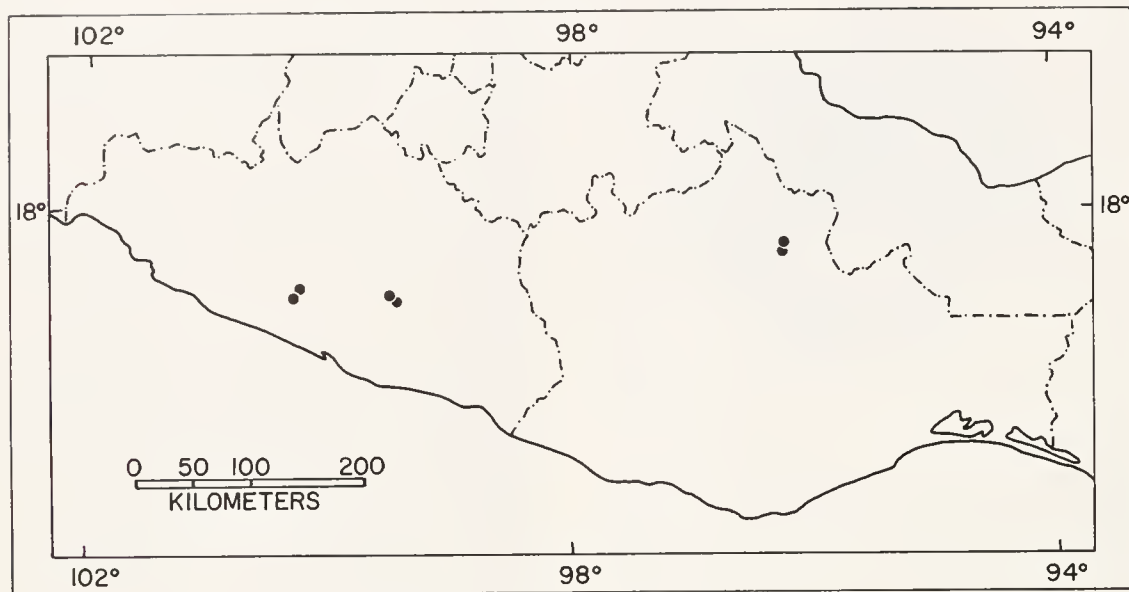
ETYMOLOGY: The specific name is derived from the Greek *erythros* meaning red, and from the Greek *omma* meaning eye; the name refers to the diagnostic red eye of this species.

DISTRIBUTION: *Hyla erythromma* is known from the Pacific slopes of the Sierra Madre del Sur at elevations of 700 to 950 meters in Guerrero, México, and from elevations of 600 to 850 meters on the northern slopes of the Sierra de Juárez in northern Oaxaca, México (fig. 198).

See Appendix 1 for the locality records of the 88 specimens examined.

The *Hyla pinorum* Group

DEFINITION: The members of this group are small stream-breeding species; males attain a maximum snout-vent length of 33.1 mm. and females, 34.6 mm. The dorsum is yellow or pale tan with dark flecks, spots, or middorsal line. The thighs are uniform yellow or tan, and the shanks and forearms are marked by flecks or narrow transverse bars. The palpebral membrane is clear. The fingers are no more than one-half webbed, and the toes are about three-fourths webbed (fig. 199). Dermal fringes and appendages are lacking on the limbs. A distinct tarsal fold

FIG. 198. Distribution of *Hyla erythromma*.

and an axillary membrane are present. The tympanum is evident (*melanomma*) or concealed (*pinorum*). Males have single, median, subgular vocal sacs and have (*melanomma*) or lack (*pinorum*) horny nuptial tuberosities on the pollices. The cranial elements are moderately well ossified; a large frontoparietal fontanelle is present. The sphenethmoid is large and extends anteriorly between the nasals (*pinorum*) or not (*melanomma*). The nasals broadly overlap the sphenethmoid in *pinorum* and lie adjacent to it in *melanomma* (fig. 200). The quadratojugal is present, reduced to a small sliver, or absent. The squamosal is in bony contact with the crista parotica in *pinorum* and narrowly separated in *melanomma*; the anterior arm of the squamosal extends no more than one-third of the distance to the maxillary. The medial ramus of the pterygoid is not in bony contact with the prootic. Prevomerine teeth are present. The tadpoles have long, terminally rounded tails and moderately large mouths with deep lateral folds and two upper and five lower rows of teeth. The mating call consists of a series of short notes. The number of chromosomes is unknown.

COMPOSITION: Two species (*H. melanomma* and *pinorum*), the former composed of two subspecies, are included in the group,

which is restricted to the Atlantic slopes of the Chiapan highlands and the Pacific slopes of the Sierra Madre del Sur in México. Of the three taxa, 103 preserved frogs, four skeletons, and five lots of tadpoles have been examined.

COMMENTS: *Hyla pinorum* and *melanomma* are placed together mostly on the basis of the similarities of their tadpoles, which are distinctive in having two upper and five lower rows of teeth (figs. 101 and 102). Otherwise, the species are sufficiently different that they might be placed in separate groups, although neither fits closely with any of the other groups of Mexican stream-breeding hylids. In some respects, the *Hyla pinorum* group might be closely related to the more advanced *Hyla mixomaculata* group, in which the adults lack a tympanum and vocal sac, and the tadpoles have seven upper and 11 lower rows of teeth. Externally, *Hyla pinorum* resembles members of the *Hyla mixomaculata* group by having barred limbs and by lacking a tympanum and nuptial excrescences. However, it differs from members of that group by having a quadratojugal, the squamosal in bony contact with the crista parotica, much smaller nasals, an anteriorly notched sphenethmoid, and a vocal sac. *Hyla melanomma* differs from the species in the

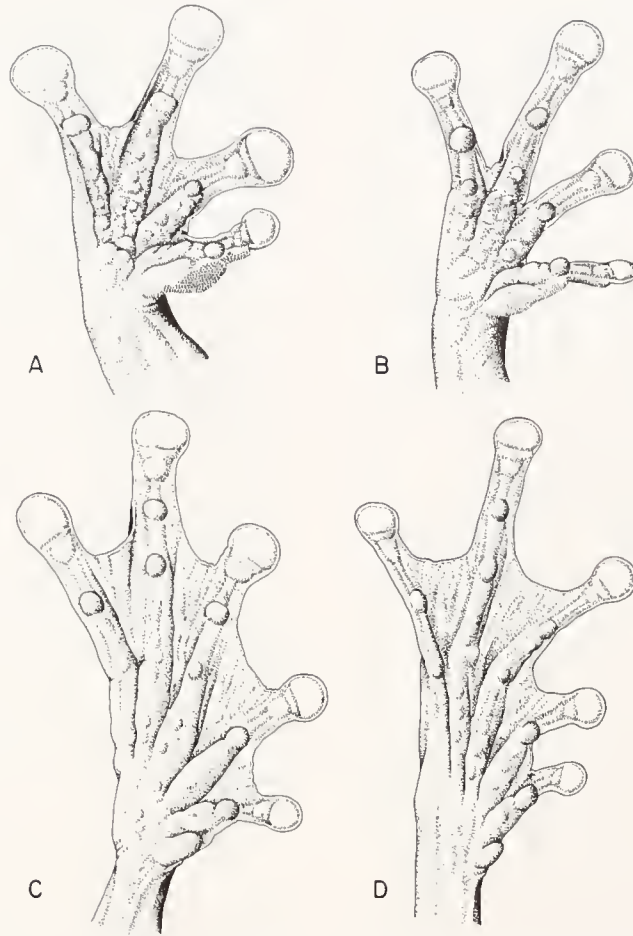


FIG. 199. Hands and feet of members of the *Hyla pinorum* group. A and C. *Hyla melanomma melanomma*, K.U. No. 86949. B and D. *Hyla pinorum*, U.M.M.Z. No. 125369. $\times 5$.

Hyla mixomaculata group by having a tympanum, nuptial excrescences in breeding males, and no transverse bars on the limbs. The cranium of *H. melanomma* resembles those of members of the *Hyla mixomaculata* group, except that in the former the nasals are rather narrowly separated and lie anterior to the sphenethmoid.

Hyla pinorum possibly evolved on the Pacific slopes of the Sierra Madre del Sur at a time when *melanomma* was isolated on the Atlantic slopes of the Chiapan highlands. Subsequently, *melanomma* probably migrated into the Sierra Madre del Sur, leaving behind a population in Chiapas that differentiated slightly, thereby giving rise to the subspecies

bivocata in Chiapas and *melanomma* in the Sierra Madre del Sur.

Hyla melanomma Taylor

Hyla melanomma Taylor, 1940d, p. 508.

DIAGNOSIS: This small species has uniformly yellow thighs and a distinct axillary membrane. The only other Middle American hylid having these characters is *Hyla ebracata*, which has a more extensive axillary web and usually a dark hourglass-shaped mark on the dorsum. The dorsal markings in *melanomma* consist of small dark flecks. *Hyla melanomma* is most easily confused with *Hyla sumichrasti*, which has similar coloration and

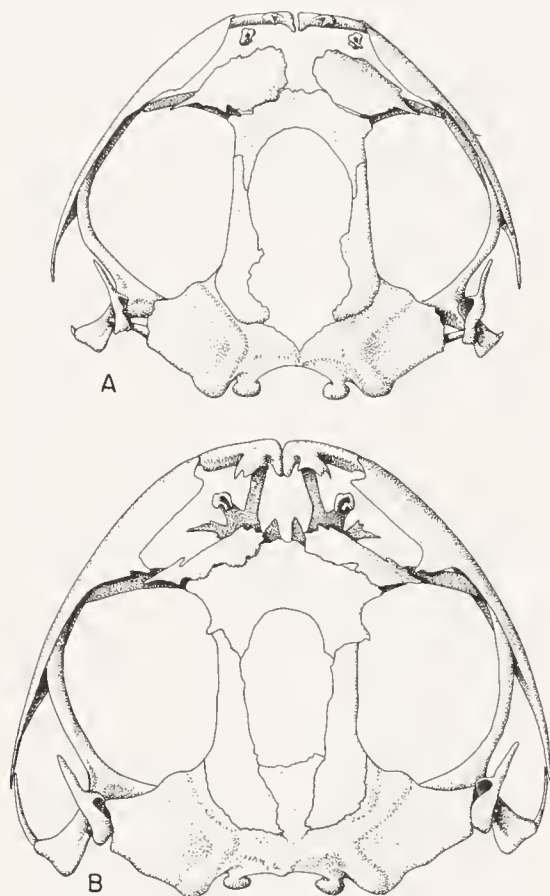


FIG. 200. Dorsal views of skulls. A. *Hyla melanomma*, K.U. No. 86953. B. *Hyla pinorum*, U.M.M.Z. No. 125367. $\times 6$.

an abbreviated axillary membrane, but differs from *melanomma* by having a shorter anal sheath and usually no more than two teeth on each prevomerine process (*melanomma* usually has four or five teeth). Considerable differences obtain in the skulls and tadpoles (see respective descriptions). See the diagnoses and descriptions of the subspecies for further characteristics and comparisons.

CONTENT: Two subspecies are recognized: *Hyla m. melanomma* Taylor inhabits the Pacific slopes of the Sierra Madre del Sur in México and *H. m. bivocata* Duellman and Hoyt occurs on the Atlantic slopes of the Chiapan highlands in México.

Although minor differences exist in the amount of webbing, size, and in certain parameters of the mating calls, the size of the

tympanum relative to that of the eye and the amount and distribution of dark pigment on the dorsum are the major differences between the subspecies. The Chiapan subspecies (*H. m. bivocata*) has a small tympanum (less than 43 per cent of the eye) and few large dark flecks on the body, whereas the nominate subspecies in the Sierra Madre del Sur has a larger tympanum (50 per cent or more of the eye) and many small dark flecks on the body and shanks.

DISTRIBUTION: *Hyla melanomma* occurs at elevations of 900 to 2000 meters on the Pacific slopes of the Sierra Madre del Sur in Guerrero and Oaxaca and on the Atlantic slopes of the Chiapan highlands, México (fig. 203).

Hyla melanomma melanomma Taylor

Hyla melanomma Taylor, 1940d, p. 508 [holotype, F.M.N.H. No. 100074 (formerly E.H.T.-H.M.S. No. 21578) from 11 kilometers east of Chilpancingo, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 89.

Hyla bivocata oaxacae Lynch, in Smith, Langebartel, and Williams, 1964, p. 23 [nomen nudum].

Hyla melanomma melanomma: Duellman, 1966b, p. 272.

DIAGNOSIS: This subspecies can be distinguished from other species of Middle American hylids by means of the characters given in the diagnosis of the species and from the subspecies *bivocata* by having a larger tympanum (tympanum/eye ratio in *melanomma* is more than 0.500 and in *bivocata*, less than 0.430) and more numerous and smaller dark flecks on the dorsum.

DESCRIPTION: Males of this subspecies attain a maximum snout-vent length of 29.9 mm., and females reach 31.5 mm. In a series of 19 males from streams at 910 and 1040 meters above (north of) San Gabriel Mixtepec, Oaxaca, México, the snout-vent length is 26.7 to 28.3 (mean, 27.4) mm.; the ratio of tibia length to snout-vent length is 0.482 to 0.527 (mean, 0.505); the ratio of foot length to snout-vent length is 0.410 to 0.446 (mean, 0.430); the ratio of head length to snout-vent length is 0.300 to 0.337 (mean, 0.327); the ratio of head width to snout-vent length is 0.318 to 0.345 (mean, 0.330), and the ratio of the diameter of the tympanum

to that of the eye is 0.500 to 0.667 (mean, 0.590). In seven males from the vicinity of Agua del Obispo, Guerrero, México, the snout-vent length is 25.1 to 29.9 (mean, 27.1) mm.; in three females from the same locality, the snout-vent length is 29.2 to 31.5 (mean, 30.1) mm. In the males from Agua del Obispo, the ratio of the diameter of the tympanum to that of the eye is 0.500 to 0.516 (mean, 0.509).

The head is as wide as the body, and the top of the head is slightly convex. In dorsal profile, the snout is acuminate; in lateral profile, it is bluntly rounded. The snout is long, and the slightly protuberant nostrils are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is rounded and barely evident; the loreal region is barely concave, and the lips are moderately thick and not flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum; a vertical fold of skin obscures the posterior rim of the tympanum, which otherwise is distinct and separated from the eye by a distance equal to about two-thirds of the diameter of the tympanum.

The arms are moderately long and slender; an axillary membrane extends to the middle of the upper arm. A weak, tubercular fold is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist. The fingers are short and bear moderately large discs; the width of the disc on the third finger is equal to the diameter of the eye. The subarticular tubercles are moderately large and subconical; the distal tubercle on the fourth finger is barely bifid in most individuals. The supernumerary tubercles are small, subconical, and irregularly arranged on the basal segments of each digit. A tripartite palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears a horny nuptial excrescence. The fingers are about one-half webbed (fig. 199A). The webbing is vestigial between the first and second fingers, but extends from the middle of the penultimate phalanx of the second to the distal end of the antepenultimate phalanx of the third and

on to the distal end of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibio-tarsal articulation extends to the eye. A few small tubercles are present on the heel, and a distinct tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is low, flat, elliptical, and broader basally than distally. The toes are moderately long and slender and bear discs that are slightly smaller than those on the finger. The sub-articular tubercles are moderately large and subconical. The supernumerary tubercles are moderately large, subconical, and present in a single row on the proximal segment of each digit. The toes are about three-fourths webbed (fig. 199C). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally near the upper level of the thighs. A short, heavy anal sheath is present. Numerous large tubercles are present below the anal opening. The skin on the dorsal surfaces of the body and limbs, and on the ventral surfaces of the arms and shanks is smooth; that on the throat, belly, and ventral surfaces of the thighs is heavily granular. The tongue is broadly cordiform, barely notched posteriorly, and only slightly free behind. The dentigerous processes of the prevomers are widely separated, posteromedially inclined elevations between the moderately small, ovoid choanae. There are three to five teeth on each elevation. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla melanomma melanomma* consists of a pale brown or yellowish tan dorsum with scattered small olive-brown or dark brown flecks (pl. 58, fig.



FIG. 201. Tadpoles of members of the *Hyla pinorum* group. A. *Hyla melanomma melanomma*, K.U. No. 87608. B. *Hyla pinorum*, K.U. No. 87611. $\times 3$.

1). At night, the dorsum is pale yellowish tan with little indication of dorsal markings. By day, the dorsal ground color darkens to a darker tan or pale brown, and the dark flecks are evident on the body and dorsal surfaces of the limbs. A dark brown canthal stripe is evident in most individuals, which usually also have a dark brown line along the supratympanic fold, and a series of interconnected brown spots along the flank. Ventral to this series of spots, the flank is creamy white. The anterior and posterior surfaces of the thighs are dull yellow, and the belly is creamy white. A faint white anal stripe is present in most individuals. The iris varies from a pale bronze to a deep bronze lightly flecked with black.

In preservative, the dorsum is pale grayish tan or pale brown with dark brown or black flecks on the forearm, body, and shanks. The flanks, thighs, and ventral surfaces are creamy tan.

TADPOLES: Five tadpoles in developmental stage 25 have body lengths of 7.1 to 7.4 (mean, 7.2) mm. and total lengths of 16.7 to 17.3 (mean, 16.9) mm. The largest tadpole, in developmental stage 38, has a body length of 13.8 mm. and a total length of 36.9 mm. A typical tadpole in developmental stage 36 has a body length of 12.6 mm. and a total length of 36.2 mm. The body is streamlined, noticeably tapered posteriorly. The body is slightly wider than deep. In dorsal profile, the snout is bluntly rounded, and in lateral profile, it is round. The eyes are large, widely separated, and directed dorsolaterally. The

nostrils are directed anterolaterally at a point about two-fifths of the distance from the eyes to the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point well below the midline and about two-thirds of the distance from the snout to the posterior end of the body. The anal tube is short and dextral. The caudal musculature is moderately heavy and extends nearly to the tip of the acutely rounded tail. The fins are moderately shallow; at midlength of the tail, the depth of either fin is approximately equal to the depth of the caudal musculature. The dorsal fin does not extend onto the body (fig. 201A).

In preservative, the body is dull grayish brown; ventrally, small white flecks are evident. The tail is creamy tan with minute dark flecks on the musculature and fins.

The mouth is ventral and medium in size; the width of the mouth is equal to about one-half of the greatest width of the body. Deep lateral folds are present in the lips, which are completely bordered by a single row of long, slender papillae. Additional papillae are present in the lateral folds. The beaks are moderately robust and bear long blunt serrations. The upper beak is in the form of a broad arch with slender lateral processes; the lower beak is broadly V-shaped. There are two upper and five lower rows of teeth. The upper rows are long; the second upper row is narrowly interrupted medially. The first four lower rows are as long as the upper ones and complete; the fifth lower row is somewhat shorter than the others (fig. 202A).

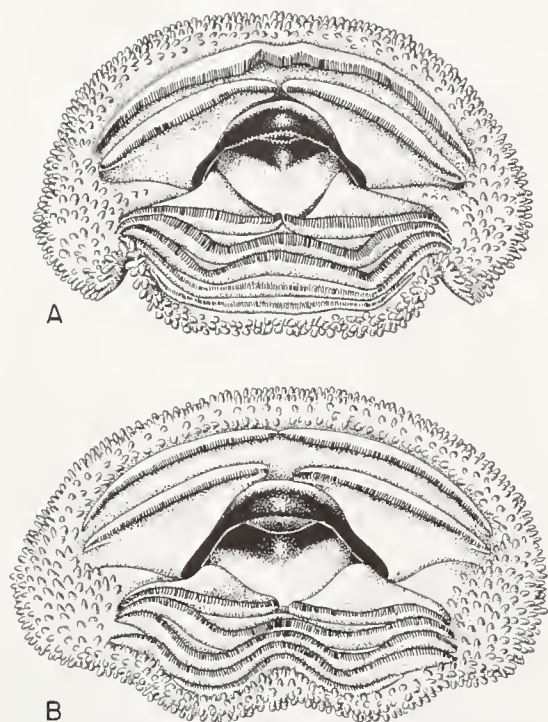


FIG. 202. Mouths of tadpoles of members of the *Hyla pinorum* group. A. *Hyla melanomma melanomma*, K.U. No. 87608. B. *Hyla pinorum*, K.U. No. 87611. $\times 15$.

MATING CALL: The mating call of *Hyla melanomma melanomma* consists of a series of quickly repeated short notes interspersed by individually produced long notes. The repetition rate of the short notes varies from 71 to 90 (mean, 78) notes per minute. The duration of each note is 0.07 to 0.08 of a second, and the interval between notes varies from 0.45 to 0.50 of a second. There are approximately 300 pulses per second in these notes which have a fundamental frequency of 163 to 217 (mean, 190) cycles per second and dominant frequency of 2286 to 2387 (mean, 2336) cycles per second (pl. 17, fig. 2).

Recordings of the long note produced by one individual provides the following data: the duration of the note is 0.31 to 0.37 of a second. The pulse rate is about 220 pulses per second; the fundamental frequency is about 139 cycles per second, and the dominant frequency is about 2112 cycles per second. Most calling males produce a series of

short notes; one or two long notes are interspersed in the series of short notes, or a series of short notes is followed by several long notes. One individual was observed to produce solely long notes. Another individual produced 28 short notes in 20 seconds; these were followed immediately by three long notes.

NATURAL HISTORY: *Hyla melanomma melanomma* inhabits cloud forest and pine-oak forest, where this species breeds in small streams. Calling males have been observed in low trees and bushes along, or overhanging, small streams. Calling males have been observed in the months of June, July, and August. Taylor (1940d, p. 510) noted that adults and juveniles were taken from bromeliads in low trees growing along a small stream at a locality 11 kilometers east of Chilpancingo, Guerrero, México, on August 20, 1939.

Tadpoles were obtained in shallow, gravel-bottomed pools in small rivulets at Agua del Obispo, Guerrero, México, and north of San Gabriel Mixtepec, Oaxaca, México, in June. At the latter locality on June 20, 1964, a metamorphosing young was found on a bush overhanging the stream. This individual has a snout-vent length of 15.3 mm. and a tail stub of 6.0 mm. in length.

Taylor (1940d, p. 510) noted that the dorsal coloration in life was "light olive-green, lighter on side and above limbs . . ." I have not seen living individuals so colored.

Duellman (1966b, p. 272) reported on the geographic variation in this subspecies and assigned two specimens from Campamento Vista Hermosa, Oaxaca, to *H. melanomma melanomma*. Further study of these specimens, plus additional material from the same locality revealed that the specimens from Campamento Vista Hermosa are not *Hyla melanomma*, but instead are representatives of *Hyla dendroscarta*.

ETYMOLOGY: The specific name is derived from the Greek *melanos*, meaning black, and the Greek, *omma*, meaning eye. Taylor (1940d, p. 510) used this name in reference to his observation that "the eyeball is very black and seen through the eyelid makes the eyelids appear black. . . ."

DISTRIBUTION: *Hyla melanomma melanomma* occurs at elevations of 900 to 2000

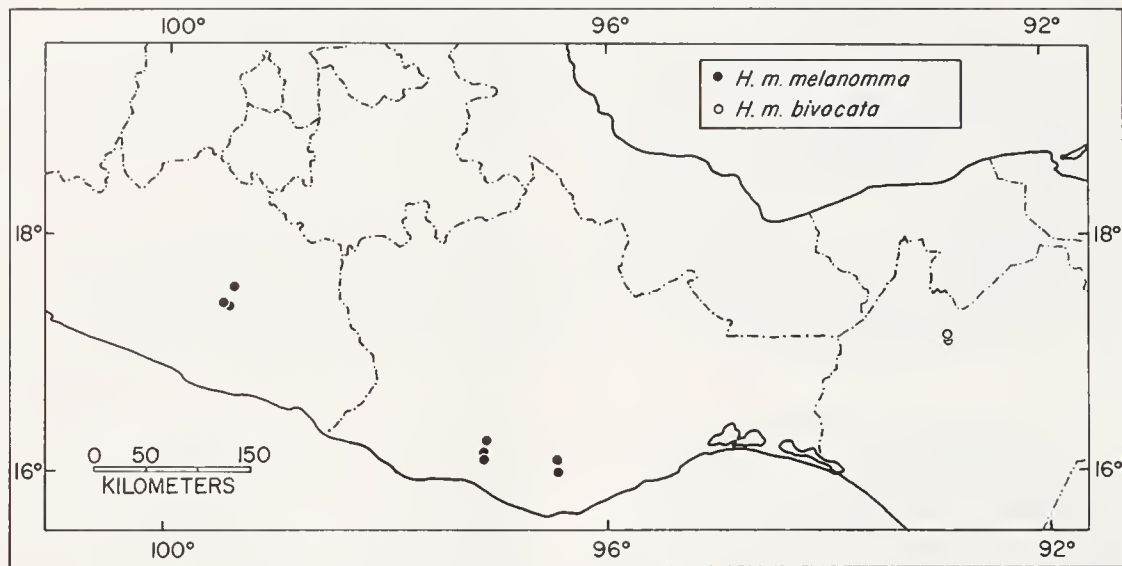


FIG. 203. Distribution of the subspecies of *Hyla melanomma*.

meters on the Pacific slopes of the Sierra Madre del Sur from central Guerrero to south-central Oaxaca, México (fig. 203).

In addition to the 79 specimens examined that are listed in Appendix 1, Smith and Brandon (1968, p. 50) reported five specimens (U.I.M.N.H. Nos. 78826-30) from 27 kilometers south of Juehatengo, Oaxaca, México.

Hyla melanomma bivocata Duellman and Hoyt

Hyla bivocata Duellman and Hoyt, 1961, p. 414 [holotype, K.U. No. 58446 from a small stream above (6.2 kilometers by road south of) Rayón Mescalapa, Chiapas, México; William E. Duellman and Dale L. Hoyt collectors].

Hyla melanomma bivocata: Duellman, 1966b, p. 272.

DIAGNOSIS: This subspecies can be distinguished from other species of Middle American hylids by means of the characters given in the diagnosis of the species and from the nominate subspecies by having a smaller tympanum (tympanum/eye ratio in *bivocata* is less than 0.430 and in *melanomma*, more than 0.500) and less flecking on the dorsum, especially on the shanks, than in *melanomma*.

DESCRIPTION: Males of this subspecies attain a maximum snout-vent length of 28.5 mm.; the single known female has a snout-

vent length of 26 mm. In a series of 10 males from streams above (south of) Rayón Mescalapa, Chiapas, México, the snout-vent length is 26.2 to 28.5 (mean, 27.1) mm.; the ratio of tibia length to snout-vent length is 0.508 to 0.547 (mean, 0.528); the ratio of foot length to snout-vent length is 0.426 to 0.447 (mean, 0.441); the ratio of head length to snout-vent length is 0.302 to 0.331 (mean, 0.319); the ratio of head width to snout-vent length is 0.323 to 0.347 (mean, 0.335), and the ratio of the diameter of the tympanum to that of the eye is 0.278 to 0.428 (mean, 0.359).

In most structural characters, *Hyla melanomma bivocata* is like the nominate subspecies, and the reader is referred to the description of that form for the details. *Hyla melanomma bivocata* differs from the nominate subspecies by having a smaller tympanum (see preceding paragraph) and by having slightly less webbing. The webbing between the first and second fingers is vestigial, and the webbing extends from the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third and on to the distal end of the antepenultimate phalanx of the fourth finger. The toes are about two-thirds webbed. The webbing extends from the middle of the penultimate phalanx of the first toe to the distal end of the antepenultimate phalanx of the second,

from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe. The number of teeth on each dentigerous process of the prevomer varies from two to four.

The general coloration of *Hyla melanomma bivocata* consists of a yellowish tan or pale brown dorsum, usually marked with bold dark spots (pl. 58, fig. 2). At night, the dorsum is pale yellow, and dorsal markings are barely evident. By day, the dorsal ground color darkens to pale tan or pale reddish brown, and dark olive-brown spots become evident. The loreal region is dark brown, and a dark brown stripe is present on the supratympanic fold. The flanks are pale yellow, and the belly is creamy yellow. The anterior and posterior surfaces of the thighs are dull yellow. A faint white anal stripe is present. The iris is pale golden bronze with fine black flecks.

In preservative, the dorsal surfaces are pale tan and the venter is white. A black bar extends from the nostril to the eye and a faint anal stripe is present.

TADPOLES: The tadpoles of this subspecies are unknown.

MATING CALL: The call of *Hyla melanomma bivocata* consists of a series of short notes and occasional long notes. The short notes are repeated at a rate of 60 to 65 notes per minute. The notes have a duration of 0.04 to 0.10 (mean, 0.07) of a second; the interval between notes varies from 0.58 to 0.70 (mean, 0.64) of a second. The pulse rate is 220 to 260 (mean, 240) pulses per second; the fundamental frequency is 130 to 144 (mean, 137) cycles per second, and the dominant frequency is 2456 to 2470 (mean, 2463) cycles per second. The recording of a long note shows that it has a duration of 0.53 of a second and a pulse rate of 280 pulses per second. The fundamental frequency is 152 cycles per second, and the dominant frequency is 756 cycles per second (pl. 17, fig. 3).

Most males were observed to produce only series of short notes, but one individual was observed repeatedly to emit only the single

long note. Two individuals were observed to produce a long note followed by a series of short notes.

NATURAL HISTORY: *Hyla melanomma bivocata* occurs along streams in cloud forest in Chiapas. Most of the specimens have been collected along streams at night in the months of June, July, and August. Ronald G. Altig obtained seven specimens from elephant-ear plants (*Xanthosoma*) along a stream by day in June [Smith and Brandon (1968, p. 49)].

REMARKS: Duellman and Hoyt (1961) described *Hyla bivocata* and did not compare it with *Hyla melanomma*. Duellman (1966b) noted the similarity between *bivocata* and *melanomma* and assigned the former as a subspecies of the latter. Smith and Brandon (1968, p. 50) suggested that *bivocata* was specifically distinct from *melanomma*; the status of the two populations cannot be determined definitely with the use of only preserved specimens.

ETYMOLOGY: The specific name is derived from the Latin *bi-*, meaning two, and the Latin *vocatus*, meaning call, and refers to the two kinds of notes produced by these frogs.

DISTRIBUTION: *Hyla melanomma bivocata* is known only from cloud forest at elevations between 1600 and 1700 meters on the northern slopes of the central highlands of Chiapas, México (fig. 203).

In addition to the locality records of the 15 specimens listed in Appendix 1, Smith and Brandon (1968, p. 49) listed seven specimens from 25 kilometers south of Ixhuatán and three from 32 kilometers north of Jitotol, Chiapas; both localities are near the type locality.

Hyla pinorum Taylor

Hyla pinorum Taylor, 1937, p. 46 [holotype, U.I.M.N.H. No. 25049 (formerly E.H.T.-H.M.S. No. 5972) from Agua del Obispo, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 87.

Ptychohyla leonhardschultzei (in part): Duellman, 1960c, p. 191; 1963c, p. 323.

DIAGNOSIS: This small species has strongly barred limbs, except the thighs, and lacks a tympanum. The feet are about two-thirds webbed, and large tubercles are present below the anal opening. *Hyla pinorum* differs

from other tympanum-less Mexican *Hyla* by having large tubercles below the anus. The other tympanum-less species have bands on the dorsal surfaces of the thighs, except *nubicola*, which has fully webbed feet.

DESCRIPTION: Males of this species attain a maximum snout-vent length of 33.1 mm., and females reach 34.6 mm. In five males from San Andreas de la Cruz, Guerrero, México, the snout-vent length is 28.5 to 33.1 (mean, 30.3) mm.; the ratio of tibia length to snout-vent length is 0.495 to 0.520 (mean, 0.507); the ratio of foot length to snout-vent length is 0.395 to 0.423 (mean, 0.408); the ratio of head length to snout-vent length is 0.313 to 0.344 (mean, 0.325), and the ratio of head width to snout-vent length is 0.332 to 0.361 (mean, 0.347).

The head is slightly wider than the body, and the top of the head is barely convex. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is rounded. The snout is moderately long; the nostrils are noticeably protuberant and are situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is rounded; the loreal region is concave, and the lips are moderately thick and slightly flared. A thin dermal fold extends posteriorly from the eye to a point above the insertion of the arm. The tympanum is not visible through the skin.

The arms are moderately long and slender; an axillary membrane extends to the mid-length of the upper arm. A faint dermal fold is present along the ventrolateral edge of the forearm; no dermal fold is present on the wrist. The fingers are moderately long and slender and bear medium-sized discs; the width of the disc on the third finger is equal to about one-fourth of the diameter of the eye. The subarticular tubercles are moderately large and subconical; the distal tubercle on the fourth finger is barely bifid. The supernumerary tubercles are moderately large, subconical, and irregularly arranged on the proximal segments of each digit. A low, flat, bifid palmar tubercle is present. The prepollex is moderately enlarged and in breeding males does not bear a nuptial excrescence. The fingers are barely webbed (fig. 199B). The webbing is vestigial between the first and second

fingers and extends from the distal end of the antepenultimate phalanx of the second to the base of the antepenultimate phalanx of the third and on to the middle of the antepenultimate phalanx of the fourth finger. The hind limbs are moderately long and slender; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A small tubercle is present on the heel, and a weak tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, round, and elevated. An outer metatarsal tubercle is absent. The toes are long and slender and bear small discs. The subarticular tubercles are small and conical; the supernumerary tubercles are small and subconical. The toes are about two-thirds webbed (fig. 199D). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the middle of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third, from the middle of the penultimate phalanx of the third to the middle of the antepenultimate phalanx of the fourth and on to the middle of the penultimate phalanx of the fifth toe.

The anal opening is directed posteroventrally at the midlevel of the thighs and is bordered on either side by two large tubercles. The skin on the dorsal surfaces and on the ventral surfaces of the arms and shanks is smooth; that on the throat, belly, and ventral surfaces of the thighs is granular. The tongue is ovoid, slightly longer than wide, and shallowly notched anteriorly and posteriorly, or not, and not free behind. The denticulous processes of the prevomers are small, elliptical elevations between the moderately large ovoid choanae. There are three or four teeth on each elevation. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla pinorum* is pale yellowish tan with pale brown, irregular markings on the dorsum and brown transverse bars on the limbs (pl. 58, fig. 3). The dorsum varies from a pale yellowish tan to a

pale reddish tan, and the dorsal markings vary from a pale olive-brown to a reddish brown. Usually, the markings consist of irregularly connected blotches and spots, but one individual (U.M.M.Z. No. 125367) lacks spots and blotches on the dorsum and has instead a dark middorsal line (pl. 58, fig. 4); this individual has weakly defined bars on the limbs. In other specimens, narrow, transverse dark bars are present on the dorsal surfaces of all segments of the limbs. The anterior and posterior surfaces of the thighs and the flanks are creamy yellow, and the venter is creamy white. The anal tubercles are white, and the iris is pale bronze with a grayish brown suffusion.

Recently metamorphosed young are colored noticeably different than the adults. The limbs are orange with brown bands, and the dorsum is marbled dark brown and yellowish tan. The posterior surfaces of the thighs are bright orange (pl. 58, fig. 7).

In preservative, the adults are pale tan with dark brown markings dorsally. The anterior and posterior surfaces of the thighs are creamy tan, and the flanks and venter are creamy white.

TADPOLES: A large developmental series of tadpoles was obtained at San Andreas de la Cruz, Guerrero, México, in June, 1964 (table 39, fig. 204). A typical tadpole in developmental stage 37 has a body length of 14.5 mm. and a total length of 41.0 mm. The body is ovoid, barely wider than deep. In dorsal profile, the snout is bluntly rounded, and in lateral profile it is more acutely rounded. The eyes are moderately large, widely separated, and directed dorsolaterally. The nostrils are directed anterolaterally at a point about midway between the eyes and the tip of the snout. The opening of the sinistral spiracle is directed posterodorsally at a point on the midline about midway on the length of the body. The anal tube is short and dextral. The caudal musculature is moderately heavy and extends nearly to the tip of the acutely rounded tail. The fins are moderately shallow; the ventral fin is not as deep as the dorsal fin which does not extend onto the body. At midlength of the tail, the depth of the caudal musculature is slightly greater than the depth of either fin (fig. 201B).

The body is dull tan with dark brown flecks and the tail is cream with brown flecks and spots. The fins are transparent and the dorsal fin is heavily flecked with brown. In preservative, the body is dark brown with faint light flecks laterally. The caudal musculature is creamy tan with brown flecks.

The mouth is ventral and medium-sized; its width is equal to about one-half of the greatest width of the body. Deep lateral folds are present in the lips. The lips are bordered by two rows of small papillae. The beaks are moderately robust and bear short, robust serrations. The upper beak forms a broad arch with moderately long, slender lateral processes. The lower beak is broadly V-shaped. There are two upper and five lower rows of teeth. The upper rows are long; in most individuals the second lower row is narrowly interrupted medially and in some specimens the first upper row is interrupted. The first four lower rows are nearly as long as the upper rows, but the fifth lower row is noticeably shorter. In some tadpoles, the first lower tooth row is narrowly interrupted medially (fig. 202B).

MATING CALL: Dr. Kraig Adler (*in litt.*) described the call of *Hyla pinorum* as "a fairly loud, guttural, coarse and low-pitched 'Braaa' or 'Braa-aaaa,' lasting a second or less. Calls were single and repeated at 3-4 minute intervals at the least."

NATURAL HISTORY: The only calling males of this species were obtained at San Andreas de la Cruz, Guerrero, México, in June, 1964, by Kraig Adler, who found them calling from low vegetation along a shallow stream.¹⁰ At that same locality, I found tadpoles in quiet pools in the stream and numerous metamorphosing young on low vegetation along the streams.

Completely metamorphosed young have snout-vent lengths of 19.7 and 21.0 mm.

REMARKS: Taylor (1937, p. 46) named *Hyla pinorum* on the basis of one immature

¹⁰ Adler revisited this locality on December 22, 1969, and obtained a large series of calling males and one clasping pair. Also, 12 specimens were taken from streams south of Puerto Gallo, Guerrero. At these last two localities Adler obtained specimens of an apparently unnamed species that resembles *H. pinorum* in size and color pattern but differs in call and flash colors.

TABLE 39

Measurements of Tadpoles of *Hyla pinorum*, with Means in Parentheses, in Relation to Developmental Stages.

Stage	N	Body Length	Tail Length	Total Length
25	25	7.0-12.5 (10.5)	12.0-24.0 (17.3)	19.5-36.0 (27.8)
26	13	12.0-13.0 (12.5)	19.0-22.5 (20.9)	31.0-35.5 (33.3)
27	9	12.0-14.5 (13.4)	20.5-26.0 (25.9)	32.5-40.5 (36.4)
28	8	12.0-15.0 (13.9)	23.0-27.5 (24.7)	35.5-41.0 (38.6)
29	5	13.5-14.5 (14.0)	22.5-25.5 (24.3)	37.0-39.5 (38.3)
30	3	13.0-15.0 (14.3)	23.0-24.5 (23.8)	36.0-39.5 (38.2)
31	1	14.5	26.5	41.0
32	2	14.5-15.0 (14.8)	26.0-27.0 (26.5)	40.5-42.0 (41.3)
33	3	15.0-15.5 (15.2)	23.0-27.0 (25.2)	38.0-42.0 (40.3)
34	2	14.0-15.5 (14.8)	26.5-28.0 (27.2)	40.5-43.5 (42.0)
35	1	16.0	28.5	44.5
36	4	15.0-16.0 (15.5)	26.5-28.5 (27.3)	41.5-44.0 (42.8)
37	6	14.5-17.0 (15.8)	26.0-28.0 (26.7)	41.0-44.5 (42.4)
38	3	14.0-16.5 (15.5)	25.5-27.0 (26.5)	41.0-43.5 (42.0)
39	2	16.5	29.5-32.5 (31.0)	46.0-49.0 (47.5)
40	6	15.0-17.5 (16.3)	24.5-32.5 (28.3)	40.5-50.0 (44.7)
41	11	15.0-18.5 (17.2)	23.0-33.5 (29.2)	38.0-50.5 (46.5)
42	2	15.5-19.5 (17.5)	25.0-31.0 (28.0)	40.5-50.5 (45.5)
43	3	15.0-17.0 (16.2)	19.5-23.0 (21.2)	36.0-40.0 (37.3)
44	3	16.5-20.0 (17.8)	7.5-15.5 (11.5)	24.5-32.0 (29.3)
45	1	16.0	8.5	24.5

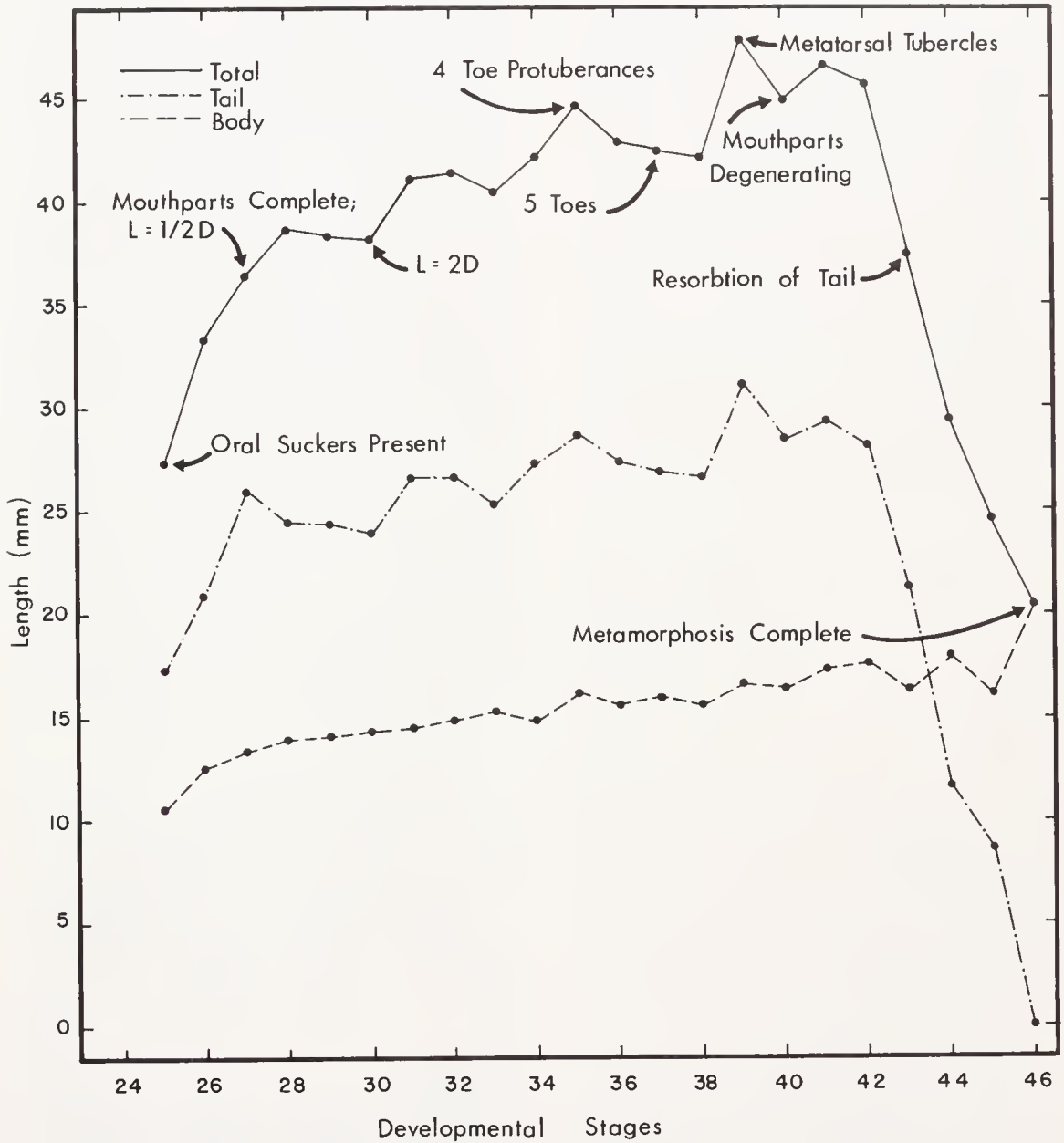


FIG. 204. Relative rate of growth in tadpoles of *Hyla pinorum* as correlated with developmental stages (table 39). Points are means of measurements given in table 1; formulas for the limb bud refer to its length (L) in relation to the basal diameter (D).

female from Agua del Obispo, Guerrero. Duellman (1960c, p. 191) considered the holotype of *Hyla pinorum* to represent an immature individual of *Ptychohyla leonhardschultzei*. The acquisition of fresh material and adults of *Hyla pinorum* definitely show that this species is valid.

ETYMOLOGY: The specific name is the genitive of the Latin *pinus*, meaning pine, and refers to the habitat of this species at Agua del Obispo, Guerrero, México.

DISTRIBUTION: *Hyla pinorum* is known from cloud forest and pine-oak forest at elevations between 700 and 1070 meters on the Pacific slopes of the Sierra Madre del Sur from central Guerrero to southwestern Oaxaca, México (fig. 205).

See Appendix 1 for the locality records of the 18 specimens examined.

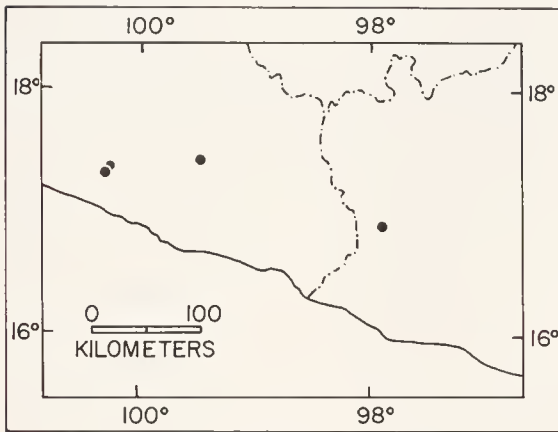


FIG. 205. Distribution of *Hyla pinorum*.

The *Hyla sumichrasti* Group

DEFINITION: The members of this group are small, stream-breeding species with broad flat heads and pointed snouts; males attain a maximum snout-vent length of 28 mm. and females, 33 mm. The dorsum is yellow, tan, gray, or green with or without dark brown or black flecks or reticulations. The thighs are dull yellow. The palpebral membrane is clear. The fingers are about one-third webbed, and the toes are about three-fourths webbed. Dermal fringes are lacking; an abbreviated axillary membrane is present. The tympanum is barely distinct. Males have single, median,

subgular vocal sacs and horny nuptial excrescences on the pollices. The skull is characterized by a large frontoparietal fontanelle and massive nasals that are broadly in contact medially (fig. 206). The sphenethmoid is short and broad. The anterior arm of the squamosal is long and extends half of the distance to the maxillary. The quadratojugal is absent, and the palatine is slender. The prevomer is broad and bears a small dentigerous process. The median ramus of the pterygoid is moderately robust but not in bony contact with the prootic. Prevomerine teeth are few in number or absent. The tadpoles have depressed bodies and long muscular tails. The mouth is immense and is bordered by three complete rows of papillae. There are three upper and seven lower rows of teeth. The mating call consists of a series of short, quickly repeated notes. The haploid number of chromosomes is 12 (known only in *H. smaragdina*).

COMPOSITION: Two species (*H. smaragdina* and *sumichrasti*) comprise the group, which is endemic to México. Of the two species, 317 preserved frogs, seven skeletons, and six lots of tadpoles have been examined.

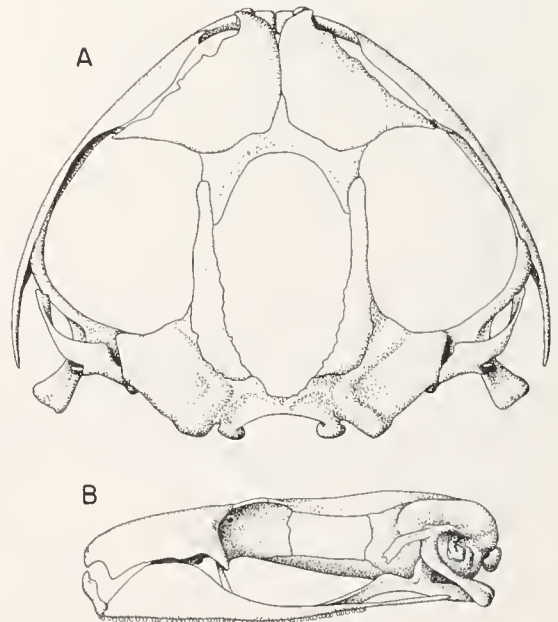


FIG. 206. Dorsal (A) and lateral (B) views of the skull of *Hyla sumichrasti*, K.U. No. 59929. $\times 6$.

COMMENTS: The two species comprising the *Hyla sumichrasti* group are alike, and differ from other Middle American hylids, by having tadpoles with immense mouths and 3/7 tooth rows. Neither by cranial characters nor by larval features can the members of this group be closely associated with other Middle American stream-breeding hylids. The skulls of *Hyla sumichrasti* and *smaragdina* bear some resemblance to those of the frogs of the *Hyla smithii* group. On the other hand, the pond-inhabiting tadpoles of the *Hyla smithii* group are distinctly different from the tadpoles of the *sumichrasti* group. Perhaps the *sumichrasti* group represents a stream-adapted stock that evolved from the *smithii* group or its ancestral stock.

The differences between *Hyla sumichrasti* and *smaragdina* are slight, and perhaps the two are conspecific. However, a large hiatus exists between their geographic ranges. Seemingly, suitable habitat is present in this hiatus (Guerrero and western Oaxaca), but despite extensive collecting in Guerrero, neither species has been found there.

Hyla sumichrasti (Brocchi)

Exerodonta sumichrasti Brocchi, 1879, p. 20 [holotype, formerly in M.N.H.N., presumably lost (*vide* Kellogg, 1932, p. 181), from Santa Efigenia, Oaxaca, México; Francis Sumichrast collector]. Brocchi, 1882.

Hylella platycephala Cope, 1879 [syntypes, U.S.N.M. No. 10037 (five specimens) from Santa Efigenia, Oaxaca, México; Francis Sumichrast collector].

Hylella sumichrasti: Boulenger, 1882a, p. 366. Günther, 1901 (1885-1902), p. 286. Kellogg, 1932, p. 181. Smith and Taylor, 1948, p. 76.

Hyla sumichrasti: Nieden, 1923, p. 249.

DIAGNOSIS: This small species has a uniformly yellow, tan, gray, or pale green dorsum and dull yellow thighs. The head is broad and flat, and the snout is pointed in dorsal profile. *Hyla sumichrasti* can be distinguished from other small yellow or tan hylids having yellow thighs by having an indistinct tympanum and by lacking a tarsal fold, extensive axillary membrane, and dorsolateral light stripes or dark dorsal markings. *Hyla smaragdina* differs by having a distinct tympanum and a tarsal fold and by usually having dark flecks or reticulations on the dorsum.

DESCRIPTION: Males of this small species at-

tain a maximum snout-vent length of 27.7 mm., and females reach 33.0 mm. In a series of 23 males from 2 kilometers northwest of Pueblo Nuevo Solistahuacán, Chiapas, México, the snout-vent length is 24.8 to 27.7 (mean, 26.2) mm.; the ratio of tibia length to snout-vent length is 0.463 to 0.556 (mean, 0.505); the ratio of foot length to snout-vent length is 0.390 to 0.460 (mean, 0.424); the ratio of head length to snout-vent length is 0.295 to 0.327 (mean, 0.311); the ratio of head width to snout-vent length is 0.285 to 0.324 (mean, 0.305), and the ratio of the diameter of the tympanum to that of the eye is 0.593 to 0.864 (mean, 0.688). In 17 females from the same locality, the snout-vent length is 28.5 to 33.0 (mean, 30.2) mm. In most proportions, the females do not differ significantly from the males, except that in the females, the ratio of the diameter of the tympanum to that of the eye is 0.652 to 0.952 (mean, 0.723). To the west, in Oaxaca, specimens are somewhat smaller. For example, in 18 males from 11.8 kilometers south of Chivela, Oaxaca, México, the snout-vent length is 23.8 to 26.0 (mean, 25.2) mm., and in 13 males from Portillo Nejapa, Oaxaca, the snout-vent length is 22.7 to 25.0 (mean, 23.9) mm. There are no significant differences in proportions, although one individual from Portillo Nejapa has a tympanum that is equal in size to the eye.

The head is as wide as the body; the top of the head is flat. The interorbital distance is about twice the width of the eyelid. In dorsal profile, the snout is somewhat pointed; in lateral profile the snout is low and round. The snout is long; the nostrils are barely protuberant and are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is rounded, and the loreal region is barely concave. The lips are thin and barely flared. A thin dermal fold extends posteriorly from the eye, above the tympanum, and downward to a point above the insertion of the arm. The fold obscures the upper one-third to one-half of the tympanum. The posteroventral edge of the tympanum is covered by skin in some specimens; otherwise, the tympanum is distinct and separated from the eye by a distance somewhat less than the diameter of the tympanum.

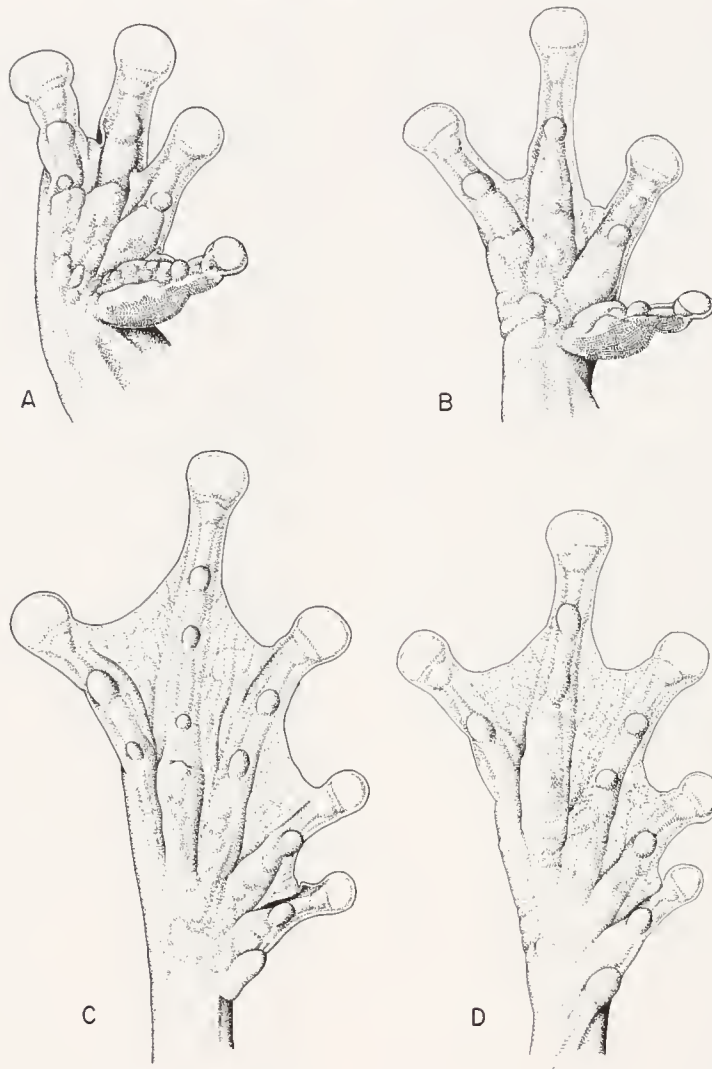


FIG. 207. Hands and feet of species in the *Hyla sumichrasti* group. A and C. *Hyla sumichrasti*, K.U. No. 57860. B and D. *Hyla smaragdina*, K.U. No. 75329. $\times 6$.

The arms are short and robust; an abbreviated axillary membrane is present. Tubercles are lacking on the ventrolateral edge of the forearm, but a distinct transverse dermal fold is present on the wrist. The fingers are short and stout and bear moderately large discs; the width of the disc of the third finger is nearly equal to the diameter of the tympanum. The subarticular tubercles are large and round; none is bifid. The supernumerary tubercles are low, round, and indistinct in some specimens. A tripartite palmar tubercle is present. The prepollex is moderately en-

larged and in breeding males bears a horny nuptial excrecence. The hands are about one-third webbed (fig. 207A). The webbing is vestigial between the first and second fingers, but connects the second finger from the base of the penultimate phalanx to the middle of the antepenultimate phalanx of the third finger and on to the base of the penultimate phalanx of the fourth. The legs are relatively short and robust; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the posterior corner

of the eye. A thin transverse dermal fold is present on the heel, but a tarsal fold is lacking. The inner metatarsal tubercle is long, low, flat, and barely visible from above; the outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are small and round, and the supernumerary tubercles are indistinct and present only on the proximal segments of each digit. The toes are about three-fourths webbed (fig. 207C). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the base of the penultimate phalanx of the third, from the distal end of the penultimate phalanx of the third to the base of the penultimate phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly near the level of the upper edges of the thighs; a short anal sheath is present. The skin on the belly and throat is granular, whereas that on other surfaces is smooth. The tongue is broadly cordiform, shallowly notched posteriorly (notched anteriorly in some specimens) and barely free behind. Of 151 specimens examined, 77 lack dentigerous processes on the prevomers. When present, the processes are short, transverse ridges between the small, round choanae. Dentigerous processes lacking teeth are present in 38 specimens, whereas one to three teeth are present on each process in 36 specimens. The vocal slits extend from the midlateral base of the tongue towards the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla sumichrasti* varies from a nearly uniform pale green or grayish green to yellowish tan or pale brown (pl. 59, figs. 1 and 2). Color notes taken on living specimens from 2 kilometers northwest of Pueblo Nuevo Solistahuacán, Chiapas, México, revealed that the dorsum varied from pale yellowish tan to olive-brown or medium brown. Minute darker flecks are present on the dorsum in some individuals. The loreal region is dark olive-green, and the anterior

and posterior surfaces of the thighs are pinkish tan. Notes on specimens from 11.8 kilometers south of Chivela, Oaxaca, México, indicate that the dorsum was pale yellow and the belly was white; the vocal sac in males is yellow. In specimens from Portillo Nejapa, Oaxaca, México, the dorsum was pale brown or pale green at night. By day, the dorsum varied from brown, grayish tan, yellowish tan, pale green, dark green, to olive-green. The belly is white, and the vocal sac is bright yellow. The flanks are pale yellow and the anterior and posterior surfaces of the thighs are dull yellowish tan. The iris is bronze with black reticulations.

In preservative, all specimens are pale brown, creamy tan, or grayish tan above. The ventral surfaces are uniform creamy tan.

TADPOLES: A typical tadpole in developmental stage 37 has a body length of 12.8 mm. and a total length of 38.5 mm. The body is depressed and about 20 per cent wider than deep. The body is tapered posteriorly in dorsal view. In dorsal profile, the snout is bluntly rounded, and in lateral profile the snout slopes gradually from the eyes to the anterior tip, which is rounded. The eyes are moderately large and directed dorsolaterally. The nostrils are situated about one-third of the distance from the eyes to the tip of the snout and are directed anterodorsally. The opening of the sinistral spiracle is slightly below the midline and at a point about two-thirds from the distance of the snout to the posterior edge of the body. The cloacal tube is long and dextral. The caudal musculature is robust and extends nearly to the tip of the rounded tail. The caudal fins are low, the dorsal fin is slightly deeper than the ventral fin. At mid-length of the tail, the depth of the caudal musculature is equal to the depth of the dorsal fin, which does not extend onto the body (fig. 208A).

The dorsum is grayish tan; bronze flecks are present on the flanks and caudal musculature. The caudal fins are transparent with faint gray blotches. The iris is pale bronze. In preservative, the tadpoles are gray with a pale creamy tan tail that is marked by faint gray blotches.

The ventral mouth is extremely large; it is as wide as the body. Definitive lateral

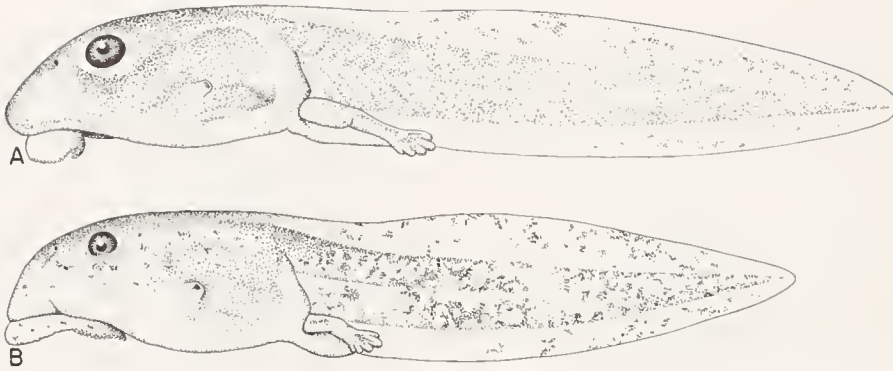


FIG. 208. Tadpoles of species in the *Hyla sumichrasti* group. A. *Hyla sumichrasti*, K.U. No. 104163. B. *Hyla smaragdina*, K.U. No. 78989. $\times 3$.

folds are lacking. The mouth is completely bordered by three rows of papillae; the papillae in the two outer rows are minute, whereas the papillae in the inner row are large and blunt. The beaks are relatively small and bear minute serrations. The upper beak forms a low arch with long, slender lateral processes. The lower beak is V-shaped. There are three upper rows and six or seven lower rows of teeth. The upper rows are equal in length; the third upper row is narrowly interrupted in some specimens. The lower rows are complete, with the exception of the seventh row, which is fragmented in all specimens in which it is present. The first four lower rows are about equal in length, but the succeeding rows are progressively shorter (fig. 209A).

Starrett (1960a, p. 28) described recently hatched tadpoles: "Larvae with external gills hatched on June 29, and by July 3, they were heavily pigmented. They measured 10-12 mm., and their mouth discs were very large." She stated that some of the tadpoles that were 10 to 12 mm. in length had tooth row formulas of $3/4$ or $3/5$.

MATING CALL: The call of *Hyla sumichrasti* consists of a series of quickly repeated notes: "haah-haah-haah." Each call group consists of 17 to 29 (mean, 24) notes. The first one to five notes in each call group are monophasic; successive notes are biphasic. The analysis of the calls of three individuals shows the duration of the notes is 0.18 to 0.21 (mean, 0.198) of a second. The pulse rate varies from 70 to 75 (mean, 71) pulses

per second. The note repetition rate varies from 125 to 170 (mean, 154) notes per second. The fundamental frequency varies from 79 to 115 (mean, 94) cycles per second. In

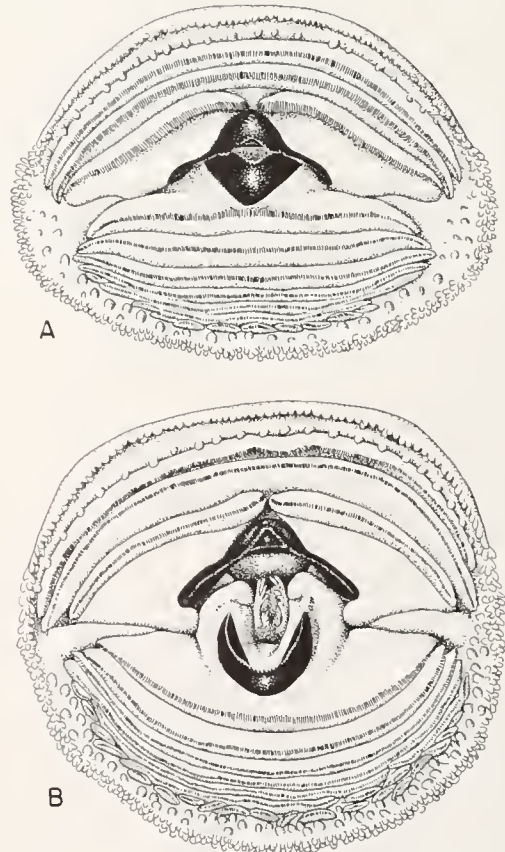


FIG. 209. Mouths of tadpoles of the *Hyla sumichrasti* group. A. *Hyla sumichrasti*, K.U. No. 104163. B. *Hyla smaragdina*, K.U. No. 78989. $\times 10$.

two individuals, the dominant frequency is at 3160 and 3220 cycles per second; another emphasized harmonic is present between 1800 and 2000 cycles per second. In the third individual, the dominant frequency is at 1830 cycles per second (pl. 18, fig. 2).

NATURAL HISTORY: *Hyla sumichrasti* inhabits subhumid oak and pine forests, where it breeds in rocky streams. In the dry season, individuals are most commonly found in arboreal bromeliads. Prior to the onset of the rains at a locality 2 kilometers northwest of Pueblo Nuevo Solistahuacán, Chiapas, México, on June 15, 1960, 40 specimens of this small frog were obtained from bromeliads in pine-oak forest. As many as five frogs were taken from one bromeliad.

On July 6, 1956, I found males calling from small bushes and rocks in and along a swift rocky stream 11.8 kilometers south of Chivela, Oaxaca, México. Calling males were found at Portillo Nejapa, Oaxaca, México, on August 9, 1966; at that locality the frogs were calling from rocks in the bed of a small stream in dry pine-oak forest. Starrett (1960, p. 28) found calling males along a rocky stream on June 27, 1957, 19 kilometers north of Arriaga, Chiapas, México. She stated: "At this time eggs and 20-mm. tadpoles were collected from the same stream. The eggs, about 50 in number, were fastened in one layer to a piece of dead leaf wedged in among rocks in the water. They were uniform grayish white in color."

REMARKS: The application of the specific names *sumichrasti* and *platycephala* was discussed by Boulenger (1891) and Kellogg (1932). The specimens forming the basis for Brocchi's description of *Exerodonta sumichrasti* and for Cope's *Hylella platycephala* were all collected by Francis Sumichrast. Brocchi's description appeared before that of Cope.

Duellman (1960b) discussed the diagnostic characters of this species as given by Taylor (1943) and Taylor and Smith (1945). He noted that the species had been incorrectly diagnosed as having no vocal sacs, rarely having prevomerine teeth, and as having a relatively smooth throat.

ETYMOLOGY: The specific name is a patronym for Francis Sumichrast, who collected the type series.

DISTRIBUTION: *Hyla sumichrasti* inhabits the Pacific slopes of eastern Oaxaca (east and west of the Isthmus of Tehuantepec) and western Chiapas, and the slopes of the Chiapan highlands, principally in the Río Grijalva drainage, México (fig. 210). This species occurs at elevations between 200 and 1675 meters.

See Appendix 1 for the locality records of the 172 specimens examined.

Hyla smaragdina Taylor

Hyla smaragdina Taylor, 1940a [holotype, F.M.N.II. No. 100009 (formerly E.H.T.-H.M.S. No. 17534) from 6 kilometers east of Cojumatlán, Michoacán, México; Edward H. Taylor collector]. Smith and Taylor, 1948, p. 90. Duellman, 1961c, p. 51 [synonymized *Hylella azteca* Taylor, 1943, with *Hyla smaragdina* Taylor, 1940a].

Hylella azteca Taylor, 1943, p. 49 [holotype, U.I.M.N.II. No. 25044 (formerly E.H.T.-H.M.S. No. 17525) from Tepoztlán, Morelos, México; Edward H. Taylor collector].

Hyla azteca: Gorham, 1963, p. 21.

DIAGNOSIS: This small species has a yellowish tan or green dorsum usually marked with dark flecks or reticulations. This coloration, together with a pointed snout, a broad and flat head, distinct tympanum, tarsal fold and the absence of an extensive axillary membrane, distinguish *smaragdina* from other Middle American hylids. *Hyla sumichrasti* has an indistinct tympanum and lacks a tarsal fold.

DESCRIPTION: Males of this species attain a maximum snout-vent length of 26 mm., and females reach 28 mm. In a series of 25 males from Santa Lucía, Sinaloa, México, the snout-vent length is 23.0 to 25.9 (mean, 24.4) mm.; the ratio of tibia length to snout-vent length is 0.434 to 0.519 (mean, 0.470); the ratio of foot length to snout-vent length is 0.352 to 0.439 (mean, 0.400); the ratio of head length to snout-vent length is 0.278 to 0.339 (mean, 0.309); the ratio of head width to snout-vent length is 0.251 to 0.292 (mean, 0.268), and the ratio of the diameter of the tympanum to that of the eye is 0.542 to 0.857 (mean, 0.683). One adult female from the same locality has a snout-vent length of 28.0 mm.; in this specimen the ratio of the diameter of the tympanum to that of the eye is 0.957.

The head is as wide as the body; the top of the head is flat, and the interorbital dis-

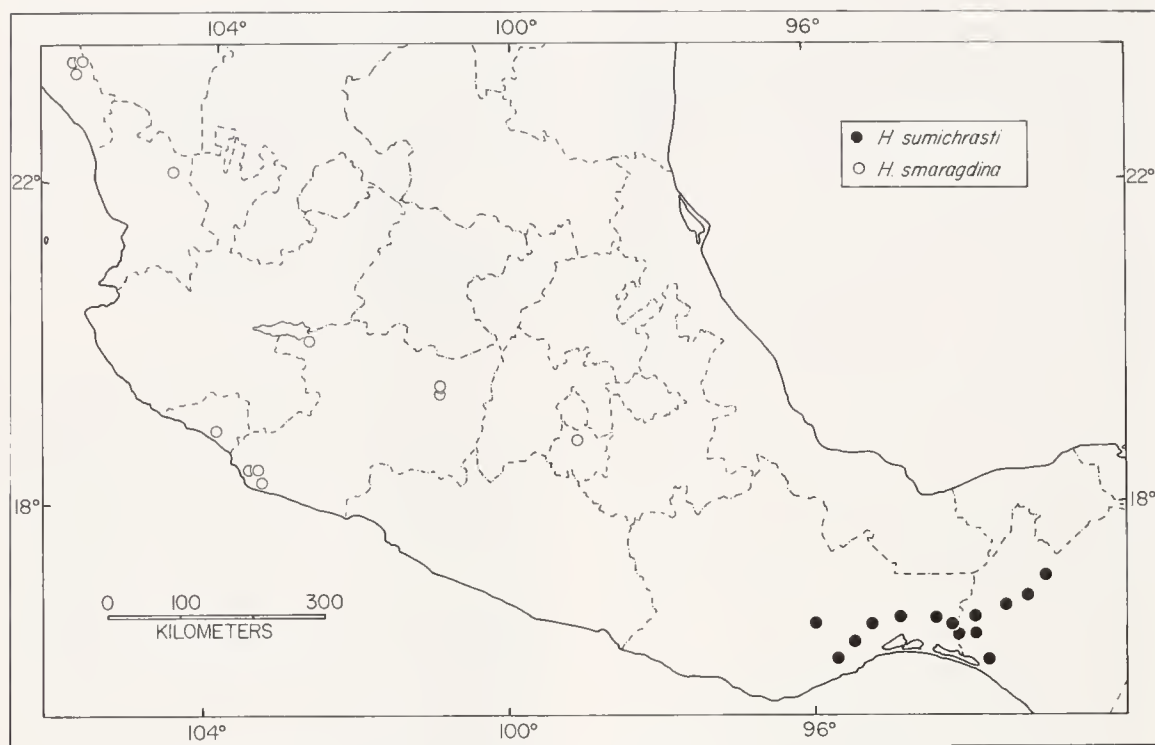


FIG. 210. Distribution of *Hyla smaragdina* and *Hyla sumichrasti*.

tance is noticeably greater than the width of the upper eyelid. In dorsal profile, the snout is pointed; in lateral profile, the snout is acutely rounded and slightly protruding. The snout is long, and the nostrils are situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is round; the loreal region is barely concave, and the lips are only slightly flared. A thin dermal fold extends posteriorly from the eye, above the tympanum and to a point above the insertion of the arm. The fold obscures the upper edge of the tympanum, which otherwise is distinct and separated from the eye by a distance less than the diameter of the tympanum.

The arms are moderately short; an abbreviated axillary membrane is present. Tubercles are absent on the ventrolateral edge of the arm, but a distinct transverse dermal fold is present on the wrist. The fingers are moderately short and bear large discs; the width of the disc of the third finger is equal to the diameter of the tympanum. The sub-articular tubercles are large and round; none

is bifid. Supernumerary tubercles, if present, are indistinct. A tripartite palmar tubercle is present. The prepollex is moderately enlarged and in breeding males bears an extensive horny nuptial excrescence. The fingers are about one-third webbed (fig. 207B). The webbing is vestigial between the first and second fingers; it extends from the base of the penultimate phalanx of the second finger to the base of the antepenultimate phalanx of the third and from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The legs are short and robust; the heels of the adpressed limbs barely overlap. The tibiotarsal articulation extends to the tympanum. A weak transverse dermal fold is present on the heel, and a moderately strong tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, round, and ovoid in outline. The outer metatarsal tubercle, if present, is small and indistinct. The toes are moderately long and bear discs that are about equal in size to those on the fingers. The subarticular tubercles are

large and round; the supernumerary tubercles usually are absent. The toes are about three-fourths webbed (fig. 207D). The webbing extends from the distal end of the penultimate phalanx of the first toe to the base of the penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the antepenultimate phalanx of the third; from the base of the disc of the third to the base of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the level of the upper edges of the thighs. A short anal sheath is present. The skin on the throat and belly is granular; elsewhere, it is smooth. The tongue is broadly cordiform, emarginate or shallowly notched behind, and barely free posteriorly. The denticulous processes of the prevomers are small transverse ridges between the small round choanac. One to three teeth are present on each ridge. The vocal slits extend from the midlateral base of the tongue to the angles of the jaws. The vocal sac is single, median, subgular, and moderately distensible.

The general coloration of *Hyla smaragdina* is pale green, yellowish green, or yellowish tan with or without dark flecks on the dorsum (pl. 59, fig. 3). All specimens from the northern part of the range (Sinaloa) are pale green or yellowish green with dark brown or black flecks on the dorsum. There is a distinct, narrow black line from the nostril to the eye; a white anal stripe is present. Individuals from the southern part of the range (Colima and Michoacán) tend to lack the dark flecks on the dorsum, which is either pale green or yellowish tan. The groin and anterior and posterior surfaces of the thighs are uniformly pinkish tan; the belly is white. The iris is gold with black flecks or reticulations.

In preservative, the dorsum varies from pale grayish tan to dull brown with or without dark flecks. The anterior and posterior surfaces of the thighs are creamy tan, and the venter is creamy white.

TADPOLES: A typical tadpole in developmental stage 37 has a body length of 13.0 mm. and a total length of 36.2 mm. The body is greatly depressed and is about 30 per cent

wider than deep. In dorsal profile the body tapers posteriorly; when viewed from above the snout is broadly rounded, and laterally it is steeply inclined to the mouth. The eyes are moderately small and directed dorsolaterally. The nostrils are noticeably closer to the eyes than to the tip of the snout. The opening of the sinistral spiracle is directed posteroventrally at a point below the midline and about two-thirds of the distance from the tip of the snout to the posterior edge of the body. The anal tube is long and dextral. The caudal musculature is robust and extends nearly to the tip of the acutely rounded tail. The caudal fins are low; the dorsal fin does not extend onto the body and is deepest at about midlength of the tail, where its depth is less than that of the caudal musculature. Throughout its length the dorsal fin is deeper than the ventral fin (fig. 208B).

In preservative, the body is gray; the caudal musculature is creamy white, and the fins are transparent. Small gray blotches are present on the caudal musculature and fins.

The mouth is immense; its width is equal to the greatest width of the body. Lateral folds are absent. The lips are completely bordered by two rows of small papillae; medial to these is a row of widely spaced larger papillae dorsally and a row of more closely spaced larger papillae along the ventral lip. The beaks are well developed and bear fine pointed serrations. The upper beak forms a low arch with long slender lateral processes; the lower beak is roughly V-shaped. There are three upper rows of teeth; these are about equal in length, and the third upper row is narrowly interrupted medially. There are six or seven lower rows of teeth, of which the first five are approximately equal in length and continuous. The sixth row is noticeably shorter and fragmented in most specimens, whereas the seventh row, if present, is fragmented in all specimens (fig. 209B).

MATING CALL: Recordings of the call of *Hyla smaragdina* are not available, but I heard the species call at Pómaro, Michoacán, México, on July 13, 1951. The call is a nasal "haah-haah-haah" repeated quickly and constantly for as long as 30 seconds.

NATURAL HISTORY: *Hyla smaragdina* inhabits tropical semi-deciduous forest and pine-

oak forest, where there is a definite dry season. Individuals have been found in bromeliads in the dry season. In the rainy season, the frogs congregate along small rocky streams. The males call from rocks in or at the edges of the stream. The tadpoles develop in the streams.

REMARKS: Duellman (1961c, p. 51) noted that Taylor (1940a, p. 18) named this species on the basis of immature individuals collected near Cojumatlán, Michoacán. Later, Taylor (1943, p. 49) named *Hylella azteca* from Tepoxtlán, Morelos. Duellman showed that the type specimens of both named taxa were representative of a single species.

Duellman (1958b, p. 8) extended the range of the species to Colima, and McDiarmid (1963, p. 7) described the tadpoles from Santa Barbara, Nayarit.

ETYMOLOGY: The specific name is Greek meaning emerald green and refers to the dorsal color of this small frog.

DISTRIBUTION: *Hyla smaragdina* occurs at elevations of about 100 to 1500 meters on the Pacific slopes of the Sierra Madre Occidental, Sierra de Coalcomán, and the Cordillera Volcánica from southern Sinaloa southward to Michoacán and Morelos, México (fig. 210).¹¹

See Appendix 1 for the locality records of the 158 specimens examined.

The *Hyla mixomaculata* Group

DEFINITION: The members of this group are small, stream-breeding species; males attain a maximum snout-vent length of 36 mm. and females, 37 mm. The dorsum is tan or brown with darker brown or black flecks or blotches. The dorsal surfaces of the limbs are banded, and the posterior surfaces of the thighs are tan or brown. The palpebral membrane is clear. The fingers are no more than one-third webbed, and the toes are at least three-fourths webbed. Dermal fringes and appendages are lacking on the limbs; an abbreviated axillary membrane is present. The tympanum is concealed (ventral edge barely evident in some *mixomaculata*). Males lack

vocal slits and horny nuptial excrescences on the pollices. The cranial elements are moderately well ossified; a large frontoparietal fontanelle is present. The sphenethmoid is large, acuminate anteriorly, and extends anteriorly between the nasals, which are moderately large, widely separated medially, and broadly sutured to, or overlapping, the sphenethmoid. The quadratojugal is absent; the squamosal is not in bony contact with the crista parotica, and the anterior arm of the squamosal extends only about one-half of the distance to the maxillary. The medial ramus of the pterygoid does not have a bony articulation with the prootic. Prevomerine teeth are present. The known tadpoles have large ventral mouths bearing seven upper and 11 lower rows of teeth. Males do not call, and the number of chromosomes is unknown.

COMPOSITION: Four species (*H. mixe*, *mixomaculata*, *nubicola*, and *pellita*) comprise the group, which is endemic to cloud forests in Veracruz and Oaxaca, México. Thirty-three preserved frogs, four skeletons, and three lots of tadpoles have been examined.

COMMENTS: Duellman (1965a, p. 34) suggested that *Hyla mixe* and *nubicola* were closely related to *mixomaculata*. These three species occur on the Atlantic slopes of the Sierra Madre Oriental in México, where *mixomaculata* and *nubicola* are sympatric in central Veracruz. *Hyla mixe* and *nubicola* are alike in having fully webbed feet and nasals that overlap the sphenethmoid, whereas in *mixomaculata*, the feet are about three-fourths webbed, and the nasals are broadly sutured to the sphenethmoid (fig. 211). *Hyla mixe* and *nubicola* apparently evolved from a *mixomaculata*-like ancestral stock, which probably also gave rise to *pellita*, a species on the Pacific slopes of Oaxaca having nasals and feet like *mixomaculata*, but differing chiefly in coloration.

The loss of voice in this group, as in other montane stream hylids, such as the *Hyla bistincta* group and *Plectrohyla*, seems to be correlated with the apparent lack of need for voice in these frogs, which throughout the year live along the streams.

Hyla mixomaculata Taylor

Hyla mixomaculata Taylor, 1950, p. 274 [holotype,

¹¹ On July 19, 1968, Dr. Robert G. Webb collected this species at 13 kilometers southeast of Izúcar de Matamoros, Puebla, thereby extending the known range farther eastward from Morelos in the upper Balsas Basin.

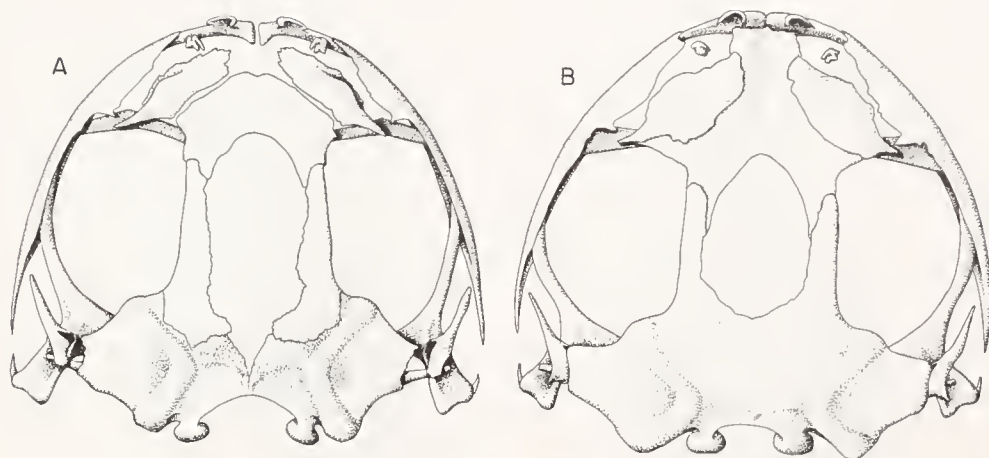


FIG. 211. Dorsal views of skulls: A. *Hyla mixomaculata*, K.U. No. 26778. B. *Hyla nubicola*, U.M.M.Z. No. S-2244. $\times 6$.

K.U. No. 26777 from Coscomatepec, Veracruz, México; Walter W. Dalquest collector].

DIAGNOSIS: This moderately small species has transverse bars on the dorsal surfaces of the limbs and feet about three-fourths webbed; it lacks a tympanum. Two of the other Mexican *Hyla* lacking a tympanum (*mixe* and *nubicola*) have fully webbed feet. *Hyla mixe* has numerous transverse bars on the limbs and robust hands and feet, and *nubicola* lacks bars on the thighs. The webbing in *mixomaculata* is similar to that in *pellita* and *pinorum*; *pellita* is smaller and has a yellowish tan, instead of a reddish brown, dorsum, whereas *pinorum* lacks transverse bars on the thighs and has large tubercles below the anal opening.

DESCRIPTION: Males of this moderately small species attain a maximum snout-vent length of 29.1 mm., and females reach 36.6 mm. In a series of three males from central Veracruz, México, the snout-vent length is 28.5 to 29.1 (mean, 28.9) mm.; the ratio of tibia length to snout-vent length is 0.491 to 0.521 (mean, 0.508); the ratio of foot length to snout-vent length is 0.459 to 0.474 (mean, 0.465); the ratio of head length to snout-vent length is 0.351 to 0.355 (mean, 0.353), and the ratio of head width to snout-vent length is 0.326 to 0.354 (mean, 0.343).

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is truncate. The snout is moderately short;

the nostrils are barely protuberant at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is angular; the loreal region is barely concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eyes to a point above the insertion of the arm. The tympanum is concealed beneath the skin; in a few specimens, the lower edge of the tympanum is barely evident.

The arms are moderately long and slender; an abbreviated axillary membrane is present. A low, glandular, dermal fold extends along the ventrolateral edge of the forearm, and a weak, transverse dermal fold is present on the wrist. The fingers are moderately short and stout and bear moderately large discs; the width of the disc on the third finger is equal to about one-third of the diameter of the eye. The subarticular tubercles are large and conical; the distal tubercles on the third and fourth fingers are bifid in some specimens. The supernumerary tubercles are small and indistinct. The palmar tubercle is low and tripartite. An elongate tubercle is present on the pollex. The prepollex is only moderately enlarged and, in males, does not bear a nuptial excrescence. The fingers are about one-third webbed (fig. 212A). The webbing is vestigial between the first and second fingers and extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from



FIG. 212. Hands of the species in the *Hyla mixomaculata* group. A. *Hyla mixomaculata*, U.M.M.Z. No. 119159. B. *Hyla pellita*, K.U. No. 100970. C. *Hyla nubicola*, K.U. No. 88031. D. *Hyla mixe*, K.U. No. 87110. $\times 5$.

the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The legs are moderately long and slender; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the eye. A distinct, transverse dermal fold is present on the heel, and an elevated, thin tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is small, flattened, ovoid, and

barely visible from above. An outer metatarsal tubercle is absent. The toes are moderately long and slender and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are moderately small and subconical, and the supernumerary tubercles are minute and indistinct in many specimens. The toes are about three-fourths webbed (fig. 213A). The webbing extends from the middle of the penultimate phalanx of the first toe to the base of the

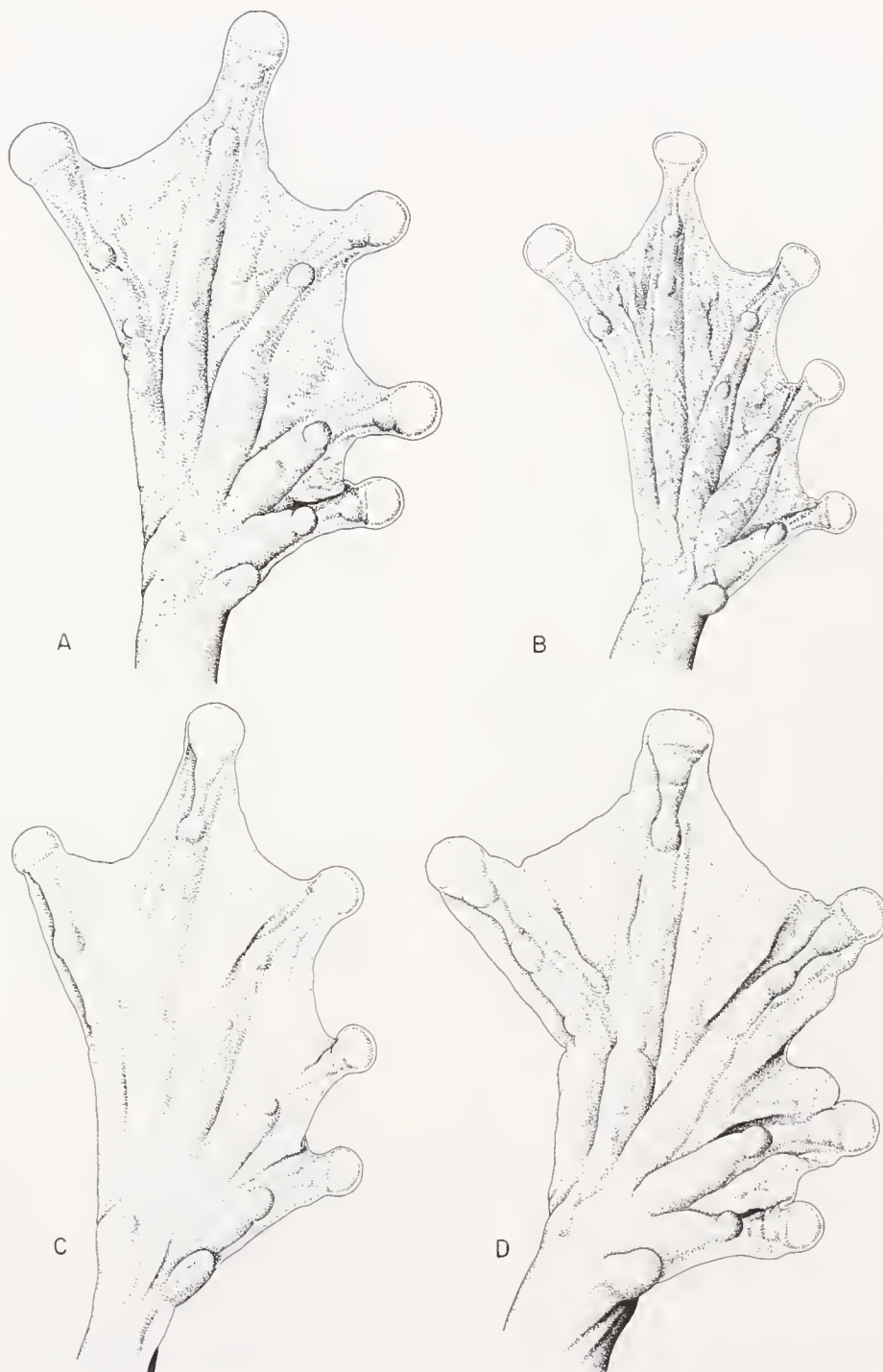


FIG. 213. Feet of the species in the *Hyla mixomaculata* group. A. *Hyla mixomaculata*, U.M.M.Z. No. 119159. B. *Hyla pellita*, K.U. No. 100970. C. *Hyla nubicola*, K.U. No. 88031. D. *Hyla mixe*, K.U. No. 87110. $\times 5$.

penultimate phalanx of the second, from the distal end of the penultimate phalanx of the second to the middle of the penultimate phalanx of the third, from the middle or distal end of the penultimate phalanx of the third to the middle of the penultimate phalanx of the fourth and on to the distal end of the penultimate phalanx of the fifth toe.

The anal opening is directed posteriorly at the level of the dorsal surfaces of the thighs. A short, unmodified anal sheath is present, and numerous tubercles are present below the anal opening. The skin on the dorsum and on the ventral surfaces of the arms and shanks is smooth, that on the throat, belly, and ventral surfaces of the thighs is granular. The tongue is cordiform, barely free behind, and shallowly notched posteriorly or not. The denticulous processes of the prevomers are narrowly separated, elliptical, transverse processes between the posterior margins of the small round choanae. There are three to five teeth on each process. Vocal slits and a vocal sac are absent.

The general coloration of *Hyla mixomaculata* is tan or pale reddish brown with darker irregular spots or blotches on the back and transverse bars on the limbs (pl. 58, fig. 5). The coloration of the dorsum is highly variable. Usually the dorsum is pale brown with a slight pinkish or reddish cast. The dorsal dark blotches are dark reddish brown. The dorsal surfaces of the limbs are tan with reddish brown transverse bars and flecks. A narrow, dark brown postorbital line is usually present. The loreal region is pale tan flecked with dark brown. The inguinal region and the posterior and anterior surfaces of the thighs are deep yellow or tan. The under surfaces of the thighs are deep yellow or tan. The under surfaces of the hind limbs are pale yellow. The webbing on the foot is pale gray. A narrow, white anal stripe is bordered below by a narrow, dark brown line. The belly is white, and the iris is coppery bronze with dark brown or black reticulations, especially peripherally.

In preservative, the dorsum is pale tan or brown with darker brown spots and blotches on the back and narrow transverse bars on the forearms, thighs, shanks, and feet. The venter is creamy white. The toes and

webbing are pale tan. Some individuals have scattered white flecks on the dorsum.

TADPOLES: A series of tadpoles obtained from a stream 3 kilometers southwest of Huatusco, Veracruz, México are referred to this species. Two tadpoles having well-developed hind limbs have the distinctive transverse bars of *Hyla mixomaculata*.

Several tadpoles in developmental stage 25 are present. The largest of these has a body length of 11.5 mm. and a total length of 32.3 mm. The largest tadpole is in developmental stage 41 and has a body length of 19.0 mm. and a total length of 49.5 mm.

A typical tadpole in developmental stage 33 has a body length of 14.4 mm. and a total length of 40.2 mm. The body is slightly depressed and slightly wider than deep. In dorsal profile, the snout is broadly rounded; in lateral profile, it is inclined anteroventrally and acutely rounded terminally. The eyes are moderately large, widely separated, and directed dorsolaterally. The nostrils are small and directed anterolaterally at a point about one-third of the distance from the eyes to the snout. The opening of the sinistral spiracle is directed posterodorsally at a point slightly below the midline about two-thirds of the distance from the snout to the posterior end of the body. The anal tube is short and dorsal. The caudal musculature is heavy and does not extend to the tip of the rounded tail. The caudal fins are moderately shallow, and the dorsal fin does not extend onto the body. The dorsal fin is slightly deeper than the ventral one. At midlength of the tail, the depth of the musculature is only slightly less than the combined depth of the dorsal and ventral fins (fig. 214).

In life the tadpoles were pale yellowish brown above and had a transparent venter. In preservative, the dorsum is dark brown, and the venter is pale gray. The caudal musculature is tan; reddish brown spots are present on the dorsal part of the musculature and on the dorsal fin.

The mouth is large, nearly as wide as the body. A slight lateral fold is present. The mouth is completely bordered by one row of small papillae. The beaks are moderately slender and lack serrations. The upper beak is in the form of a broad arch lacking lateral



FIG. 214. Presumed tadpole of *Hyla mixomaculata*, U.M.M.Z. No. 119652. $\times 3$.

processes; the lower beak is broadly V-shaped. There are seven upper and 10 or 11 lower rows of teeth, all of which are long and complete, except the seventh upper row, which is narrowly interrupted medially (fig. 215).

Tadpoles in developmental stage 25 all have seven upper rows of teeth and 10 lower rows. The outermost rows in some individuals are poorly developed. Tadpoles in developmental stage 33 all have seven well-developed upper rows and 10 or usually 11 lower rows. In the tadpoles in developmental stage 41 the outer rows of teeth have begun to degenerate, so that the first and second upper rows and the tenth and eleventh lower rows are fragmentary.

MATING CALL: The absence of vocal slits and a vocal sac precludes the presence of a mating call in this species.

NATURAL HISTORY: Most of the known specimens of *Hyla mixomaculata* have been obtained in the dry season (December, January, and February). At that time, individuals are most frequently encountered in bromeliads

in the cloud forest. On January 26, 1958, I obtained three specimens from the leaves of bushes at the edge of a stream in Barranca Metlac, Veracruz, at night.

Tadpoles were obtained on March 27, 1959; the tadpoles adhered to rocks in fast-moving parts of a clear stream.

REMARKS: The tympanum is more nearly visible in this species than in others of this group. Perhaps, this is indicative of a relatively primitive position within the group.

Hyla mixomaculata and *nubicola* occur sympatrically in central Veracruz, México. Both species have been obtained from bromeliads from the same locality on the same day.

ETYMOLOGY: The specific name is derived from the Latin *mixtus*, meaning mix, and the Latin *maculatus*, meaning spots, and refers to the interconnected spots on the dorsum.

DISTRIBUTION: *Hyla mixomaculata* occurs in cloud forest at elevations between 900 and 1500 meters in central Veracruz, México (fig. 216).

See Appendix 1 for the locality records of the 25 specimens examined.

Hyla pellita Duellman

Hyla pellita Duellman, 1968a, p. 568 [holotype, K.U. No. 100970 from 33 kilometers north of San Gabriel Mixtepec, Oaxaca, México, 1675 meters; William E. Duellman and Linda Trueb collectors].

DIAGNOSIS: This moderately small species has transverse bars on the limbs and has the feet about three-fourths webbed; it lacks a tympanum. Two of the other Mexican *Hyla* lacking a tympanum (*mixe* and *nubicola*) have fully webbed feet. *Hyla pellita* differs from *mixomaculata* by being smaller and by having a yellowish tan, instead of a reddish brown, dorsum. *Hyla pinorum* also lacks a tympanum but differs from *pellita* by having

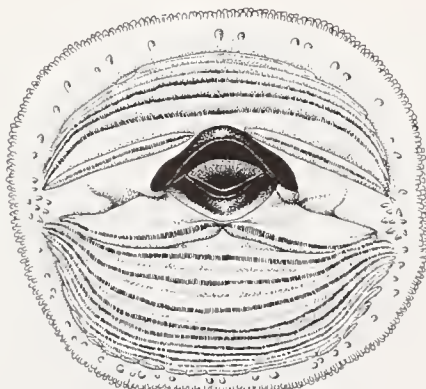


FIG. 215. Mouth of presumed tadpole of *Hyla mixomaculata*, U.M.M.Z. No. 119652. $\times 8$.

a proportionately larger head, no transverse bands on the thighs, and large tubercles below the anal opening.

DESCRIPTION: Males of this small species attain a maximum snout-vent length of 27.3

the lips are thin and moderately flared. A thin dermal fold extends posteriorly from the posterior edge of the eye to a point above the insertion of the arm. The tympanum is not visible externally.

The arms are moderately long and slender; an abbreviated axillary membrane is present. A weak tubercular fold is present on the ventrolateral edge of the forearm, but a distinct transverse dermal fold is absent on the wrist. The fingers are moderately short and stout and bear rather small discs; the width of the disc on the third finger is equal to about one-third of the diameter of the eye. The subarticular tubercles are moderately large, round, and flattened; the distal tubercles on the third and fourth fingers are bifid. The supernumerary tubercles are large, round, and present in a single row on the proximal segments of each digit. The palmar tubercle is low, flattened, and diffuse. The prepollex is barely enlarged and in males lacks a nuptial excrescence. The fingers are about one-third webbed (fig. 212B). Webbing is absent between the first and second fingers but extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, from the middle of the antepenultimate phalanx of the third to the distal end of the antepenultimate phalanx of the fourth finger. The legs are moderately long and stout; the heels of the adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the eye. A low, thin tarsal fold extends the full length of the tarsus. The inner metatarsal tubercle is flat, ovoid, and partly visible from above. The outer metatarsal tubercle is absent. The toes are moderately short and bear discs that are slightly smaller than those on the fingers. The subarticular tubercles are small and round; the supernumerary tubercles are small, flattened, and irregularly arranged on the proximal segments. The toes are about three-fourths webbed (fig. 213B). The webbing extends from the base of the disc of the first toe to the middle of the penultimate phalanx of the second, from the base of the disc of the second to the middle of the penultimate phalanx of the third, from the base of the disc of the third to the base of the penultimate

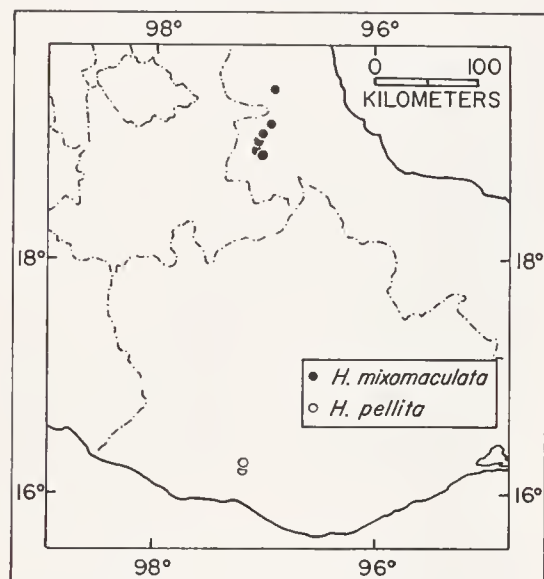


FIG. 216. Distribution of *Hyla mixomaculata* and *Hyla pellita*.

mm., and females reach 31.6 mm. In a sample of three males from the Pacific slopes of the Sierra Madre del Sur in Oaxaca, México, the snout-vent length is 25.2 to 27.3 (mean, 26.4) mm.; the ratio of tibia length to snout-vent length is 0.476 to 0.513 (mean, 0.497); the ratio of foot length to snout-vent length is 0.420 to 0.429 (mean, 0.426); the ratio of head length to snout-vent length is 0.317 to 0.327 (mean, 0.321), and the ratio of head width to snout-vent length is 0.333 to 0.341 (mean, 0.337). Two females from the same locality have snout-vent lengths of 28.6 and 31.6 mm.

The head is nearly as wide as the body, and the top of the head is flat. In dorsal profile, the snout is bluntly rounded; in lateral profile, it is truncate but rounded above. The snout is moderately long; the nostrils are barely protuberant and situated at a point about four-fifths of the distance from the eyes to the tip of the snout. The canthus is angular; the loreal region is slightly concave, and

phalanx of the fourth and on to the base of the disc of the fifth toe.

The anal opening is directed posteriorly at the level of the dorsal surfaces of the thighs. A short anal sheath has a membranous connection with the posterodorsal surfaces of the thighs. The anal opening is bordered below by vertical dermal folds and a few small tubercles. The skin on the dorsum and the ventral surfaces of the arms and shanks is smooth, that on the throat, chest, and belly is heavily granular. The tongue is cordiform, deeply notched posteriorly, and barely free behind. The denticulate processes of the prevomers are short, narrowly separated elevations between the small, round choanae. Males have three or four teeth on each elevation, and females have three to five teeth on each elevation. Vocal slits and a vocal sac are absent.

The general coloration of *Hyla pellita* is pale yellowish tan above with faintly darker tan or olive-brown markings (pl. 56, fig. 6). When active at night, the frogs are yellowish tan with reddish brown flecks. By day the coloration changed to pale brown with a dull olive-green interorbital bar, blotches on the dorsum, transverse bars on the limbs, and scattered flecks on the dorsum. The hands, feet, and anterior and posterior surfaces of the thighs are dull yellow. The belly is white. A creamy, white stripe is present on the outer edge of the forearm and another is present on the outer edge of the tarsus. A short, distinct white stripe is present above the anal opening. The iris is pale bronze.

In preservative, the dorsum is pale tan with a dark brown mark in the occipital region and dark brown marks on the back. The anterior and posterior surfaces of the thighs lack pigment. The dorsal surfaces of the arms, shanks, and feet are tan with brown transverse bars. The venter is creamy white.

All specimens have distinct transverse bars on the limbs; the number of bars on the shank varies from one to four. Two individuals are dark brown dorsally; in these the small black flecks are either not visible or are absent; flecks are present on the dorsal surfaces of four specimens that are tan or pale brown above with darker brown irregular markings.

TADPOLES: The tadpoles of *Hyla pellita* are unknown.

MATING CALL: The absence of vocal slits and a vocal sac in this species precludes the presence of a call.

NATURAL HISTORY: *Hyla pellita* has been found only along two streams in the cloud forest on the Pacific slopes of the Sierra Madre del Sur in Oaxaca, México. All individuals were found on low vegetation along streams at night. This species has been collected only in the dry season (February); visits to the type locality in the rainy season yielded no specimens.

REMARKS: Although *Hyla pellita* is included in the *Hyla mixomaculata* group, it possibly is related to *Hyla pinorum* as well. The latter species also occurs on the Pacific slopes of the Sierra Madre del Sur in Guerrero and Oaxaca. *Hyla pinorum* resembles *pellita* in size, general coloration, and in the absence of an externally visible tympanum, but differs in certain osteological characters (size of nasals, shape of the anterior end of the sphenethmoid, and in the absence of a quadratojugal).

ETYMOLOGY: The specific name is Latin, meaning covered with skin, and alludes to the complete concealment of the tympanum by the skin.

DISTRIBUTION: *Hyla pellita* is known only from elevations between 1500 and 1700 meters on the Pacific slopes of the Sierra Madre del Sur in Oaxaca, México (fig. 216).

See Appendix 1 for the locality records of the six specimens examined.

Hyla nubicola Duellman

Hyla nubicola Duellman, 1964a, p. 225 [holotype, U.M.M.Z. No. 118160 from a stream 3 kilometers southwest of Huatusco, Veracruz, México, 1325 meters; William E. Duellman collector].

DIAGNOSIS: This moderately small species has barred limbs and fully webbed feet; it lacks a tympanum. *Hyla nubicola* can be distinguished from all other tympanum-less Middle American *Hyla*, except *mixe*, by its fully webbed feet. The latter species has more robust hands and feet, many narrow bands on the limbs and pale webbing on the feet, whereas *nubicola* lacks bars on the thighs and dark webbing on the feet.

DESCRIPTION: Males of this moderately small species attain a maximum known snout-vent length of 36.7 mm., and females reach 37.3 mm. In three males from central Veracruz, México, the snout-vent length is 32.2 to 36.7 (mean, 34.2) mm.; the ratio of tibia length to snout-vent length is 0.485 to 0.515 (mean, 0.501); the ratio of foot length to snout-vent length is 0.433 to 0.450 (mean, 0.439); the ratio of head length to snout-vent length is 0.302 to 0.326 (mean, 0.313), and the ratio of head width to snout-vent length is 0.313 to 0.326 (mean, 0.320). The one known female has a snout-vent length of 37.3 mm.

The head is as wide as the body, and the top of the head is flat. In dorsal profile, the snout is truncate, but the entire head is rounded; in lateral profile, the snout is truncate and barely rounded above. The canthus is angular; the loreal region is barely concave and the lips are moderately thin and barely flared. A moderately heavy dermal fold extends posteriorly from the eye to a point above the insertion of the arm. The tympanum is covered with skin and is not visible externally.

The arms are moderately long and slender; an abbreviated axillary membrane is present. A low tubercular fold is present on the ventrolateral edge of the forearm, and a weak transverse dermal fold is present on the wrist. The fingers are short and stout and bear large discs; the width of the disc on the third finger is equal to about one-half of the diameter of the eye. The subarticular tubercles are large and round; none is bifid. The supernumerary tubercles are small and irregularly arranged on the proximal segments of each digit. The palmar tubercle is moderately large, flat, and partially bifid. A single, elliptical tubercle is present on the slightly enlarged prepollex, which lacks a nuptial excrescence. The fingers are about one-fourth webbed (fig. 212C). The webbing is lacking between the first and second fingers but extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third and from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The legs are moderately long and slender; the heels of the

adpressed limbs overlap by about one-fourth of the length of the shank. The tibiotarsal articulation extends to the anterior corner of the eye. A weak tarsal fold extends about two-thirds of the length of the tarsus. The inner metatarsal tubercle is elliptical, flat, and partly visible from above. The outer metatarsal tubercle is absent. The toes are moderately short and robust and bear discs that are noticeably smaller than those on the fingers. The subarticular tubercles are round and bluntly conical; the supernumerary tubercles are minute. The toes are fully webbed (fig. 213C).

The anal opening is directed posteriorly at the level of the upper edges of the thighs. A short, thick anal sheath is present, and small tubercles are present ventrolateral to the anal opening. The skin on the dorsum and ventral surfaces of the arms and legs is smooth; that on the throat, chest, belly, and proximal posteroventral surfaces of the thighs is weakly granular. The tongue is cordiform, wider than long, shallowly notched posteriorly, and barely free behind. The dentigerous processes of the prevomers are narrowly separated, elliptical ridges between the moderately large, ovoid choanae. There are three or four teeth on each process. Vocal slits and a vocal sac are absent.

The general coloration of *Hyla nubicola* is pale reddish brown or olive-tan with faintly darker markings on the back and limbs (pl. 58, fig. 8). The coloration in life varies from olive-tan with olive-brown markings to olive-brown with dark brown markings or reddish tan with reddish brown markings. The markings on the dorsum consist of small, irregular spots or blotches and scattered dark flecks. There are three or four dark transverse bars on the shank, and there are faint indications of transverse markings on the forearms and feet. The flanks are pale grayish tan or yellowish tan with scattered brown flecks. The venter is white; a few grayish brown flecks are present on the edge of the chin. The webbing of the feet is dark brown or dark gray. The anterior and posterior surfaces of the thighs are dull yellow or yellowish tan. A short white anal stripe is present. Small creamy white flecks are scattered on the dorsum in all specimens. The iris is coppery bronze.

In preservative, the dorsum is grayish tan with irregular dark brown blotches and spots and narrow dark brown transverse bars on the shanks. The thighs are grayish brown above; the anterior surfaces of the thighs and the ventral surfaces of the hind limbs are creamy tan and the ventral surfaces of the feet and webbing are dark brown. The flanks are pale grayish tan with brown flecks, and the belly and chin are creamy white with grayish brown flecks on the chin.

TADPOLES: The tadpoles of *Hyla nubicola* are unknown.

MATING CALL: The absence of vocal slits and a vocal sac apparently precludes a voice in this species.

NATURAL HISTORY: The few specimens of *Hyla nubicola* have been found in the vicinity of small streams in cloud forest. Individuals have been found on vegetation overhanging the streams at night and in bromeliads by day.

REMARKS: No additional information is available on this species other than that provided in the description of the species by Duellman (1964a).

ETYMOLOGY: The specific name is derived from the Latin *nubes*, meaning cloud, and the Latin suffix *-cola*, meaning an inhabitant; the name refers to the cloud forest where this species lives.

DISTRIBUTION: *Hyla nubicola* is known only from cloud forests at elevations between 900 and 1400 meters on the Atlantic slopes of the Sierra Madre Oriental in central Veracruz, México (fig. 217).

See Appendix 1 for the locality records of the six specimens examined.

Hyla mixe Duellman

Hyla mixe Duellman, 1965a, p. 32 [holotype, K.U. No. 87110 from a stream 4.2 kilometers by road south of Campamento, Vista Hermosa, Oaxaca, México, 1800 meters; David A. Johnson collector].

DIAGNOSIS: This moderately small species has strongly barred dorsal surfaces of the limbs and fully webbed feet; it lacks a tympanum. *Hyla mixe* can be distinguished from all other tympanum-less Middle American species of *Hyla* by having many narrow dark bars on the limbs. *Hyla nubicola* is the only other species that lacks a tympanum and has

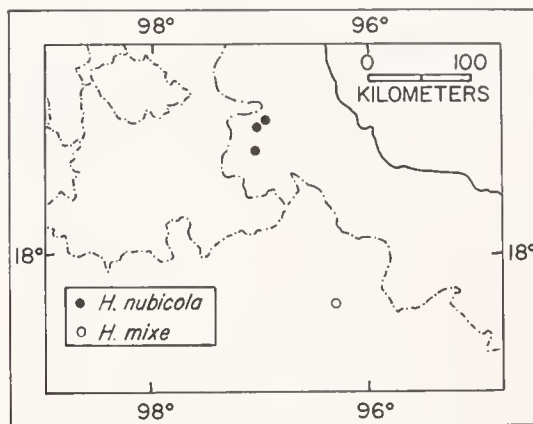


FIG. 217. Distribution of *Hyla nubicola* and *Hyla mixe*.

fully webbed feet. In comparison with *nubicola*, *mixe* has more numerous and narrower transverse bars on the limbs, a proportionately broader head with thicker lips, more robust hands and feet, and paler webbing on the feet.

DESCRIPTION: Males of this moderately small species are unknown; females attain a maximum known snout-vent length of 33.9 mm. In the two known females, the ratio of tibia length to snout-vent length is 0.495 and 0.508; the ratio of foot length to snout-vent length is 0.457 and 0.470; the ratio of head length to snout-vent length is 0.297 and 0.318, and the ratio of head width to snout-vent length is 0.330 and 0.352.

The head is as wide as the body, and the top of the head is flat. In dorsal and lateral profile, the snout is bluntly rounded. The snout is moderately long, and the nostrils are barely protuberant and situated at a point about three-fourths of the distance from the eyes to the tip of the snout. The canthus is acutely rounded; the loreal region is barely concave, and the lips are moderately thick and barely flared. A moderately heavy dermal fold extends posteriorly from the eye to a point above the insertion of the arm. The tympanum is covered by skin and is not visible externally.

The arms are moderately short and robust; an abbreviated axillary membrane is present. A distinct tubercular dermal fold is present on the ventrolateral edge of the forearm, and a distinct transverse dermal

fold is present on the wrist. The fingers are short and broad and bear moderately large discs; the width of the disc on the third finger is equal to about one-half of the diameter of the eye. The subarticular tubercles are large and round; the distal tubercle on the fourth finger is slightly bifid. The supernumerary tubercles are small, subconical, and present on the proximal segments of the digits. The palmar tubercle is moderately large and bifid; a large elliptical tubercle is present on the pollex. The prepollex is barely enlarged. The fingers are about one-third webbed (fig. 212D). The webbing is vestigial between the first and second fingers, but extends from the base of the penultimate phalanx of the second to the base of the antepenultimate phalanx of the third, and from the middle of the antepenultimate phalanx of the third to the base of the penultimate phalanx of the fourth finger. The legs are moderately long and heavy; the heels of the adpressed limbs overlap by about one-third of the length of the shank. The tibiotarsal articulation extends to the middle of the eye. A short dermal fold is present on the heel. The tarsal fold is weak and extends about one-third of the length of the tarsus. The inner metatarsal tubercle is large, flat, triangular in outline, and not visible from above. The outer metatarsal tubercle is lacking. The toes are moderately long and bear discs that are only slightly smaller than those on the fingers. The subarticular tubercles are round, and the supernumerary tubercles are moderately large and round. The toes are fully webbed (fig. 213D); a thin fold of skin extends along the outer edges of the first and fifth toes.

The anal opening is directed posteriorly at the level of the upper surfaces of the thighs. A short anal sheath is present, and small tubercles are present below the anal opening. The skin on the dorsal surfaces is slick and smooth; the skin on the ventral surfaces of the limbs is smooth, and that on the belly and ventral and posterior surfaces of the thighs is granular. The tongue is cordiform, slightly notched posteriorly, and barely free behind. The denticulous processes of the prevomers are elliptical ridges between the posterior margins of the small, ovoid choanae. There are two or three teeth on each process.

The general coloration of *Hyla mixe* is brown with darker brown markings (pl. 1, fig. 2). At night, the frogs are brown with dark brown markings, but by day they change to have a greenish tan dorsum with olive-green markings. The anterior and posterior surfaces of the thighs are tan, and the webbing is orange-tan. The venter is creamy yellow, and the iris is pale silvery green. The dorsal markings consist of irregularly interconnected spots on the back and many distinct, narrow transverse bars on the limbs. A few brown flecks are present on the flanks. A faint anal stripe is present.

In preservative, the dorsum is pale pinkish brown with dark brown markings. The flanks are white with small brown flecks. The proximal surfaces of the upper arm lack pigment, except for a few scattered brown flecks. The thighs are a pale creamy tan anteriorly and posteriorly, and marked with small brown flecks posteriorly. The ventral surfaces of the limbs and webbing are cream, and the belly and chin are white.

TADPOLES: A series of tadpoles, presumably of this species, was obtained from the type locality, a small stream in the north slope of the Sierra de Juárez in northern Oaxaca, México, on February 16, 1966. The largest preserved tadpole is in developmental stage 32 and has a body length of 13.7 mm. and a total length of 39.0 mm. The body is depressed and slightly wider than deep. The snout is broadly rounded in dorsal profile; in lateral profile, the snout slopes gradually from the nostril to an acutely rounded tip. The eyes are moderately large, widely separated, and directed dorsolaterally. The small nostrils are directed anterolaterally at a point about one-third of the distance from the eyes to the tip of the snout. The opening of the sinistral spiracle is directed posteriorly at a point slightly below the midline about two-thirds of the distance from the snout to the posterior edge of the body. The anal tube is short and dextral. The caudal musculature is robust and does not quite reach the tip of the rounded tail. The caudal fins are shallow; at midlength of the tail the depth of the caudal musculature is equal to the combined depths of the ventral and dorsal fins. The dorsal fin does not extend onto the body (fig. 218).

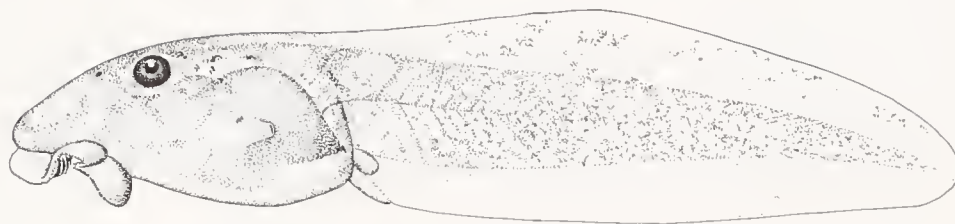


FIG. 218. Presumed tadpole of *Hyla mixe*, K.U. No. 104183. $\times 3$.

The body is dark brown with golden flecks. The tail is pale cream, and the iris is dull brown. In preservative, the body is dark brown above and dark gray below with small bluish white flecks. The caudal musculature is cream with a few brown blotches, especially dorsally. The fins are transparent, with or without faint reticulations.

The mouth is ventral and large; it is wider than the snout and as wide as the widest part of the body. A slight lateral fold is present in the lips, which are completely fringed by one row of small papillae. A few additional papillae are present laterally. The beaks are slender and nearly smooth; there are no serrations. The upper beak is in the form of a shallow curve and lacks lateral processes; the lower beak is broadly V-shaped. Typically, there are seven upper rows and 10 or 11 lower rows of teeth. All of the rows are long and extend to the edges of the lips. The seventh upper row is narrowly interrupted medially, and in some specimens the first lower row is narrowly interrupted medially. The teeth in the outer rows are short and less completely keratinized than those in the inner rows (fig. 219). Small tadpoles in develop-

mental stage 25 and having body lengths of less than 11 mm. have only 10 lower rows of teeth. Larger tadpoles in developmental stage 32 had 11 rows. The eleventh row is fragmented in some specimens. In two tadpoles there are fragments of an eighth upper row present.

The assignment of these tadpoles to *Hyla mixe* is done on the basis of their similarity of the supposed tadpoles of *Hyla mixomaculata*. Furthermore, these tadpoles were obtained at the type locality of *Hyla mixe*, a stream known to be inhabited by three other species of stream-breeding hylids, the tadpoles of all of which are known.

NATURAL HISTORY: The two known adults of *Hyla mixe* were found at night on limbs of bushes overhanging a cascading mountain stream in cloud forest. The tadpoles were obtained from the rocky stream, where they were common in midparts of the stream with rocky or gravel bottoms. The tadpoles hold on to the lee-sides of rocks with their large mouths. When disturbed they sought refuge between and under large rocks. When the tadpoles were placed in a glass container they adhered to the sides of the container with their mouths.

REMARKS: *Hyla mixe* seems to be most closely related to *Hyla nubicola* from which it differs by having more robust limbs, hands, and feet and by having numerous and distinct transverse bands on all segments of the limbs.

ETYMOLOGY: The specific name refers to the Mixe Indians that inhabit the lower mountainous regions in northern Oaxaca.

DISTRIBUTION: *Hyla mixe* is known only from a stream at an elevation of 1800 meters on the northern slopes of the Sierra de Juárez in northern Oaxaca, México (fig. 217).

See Appendix 1 for the locality records of the three specimens examined.

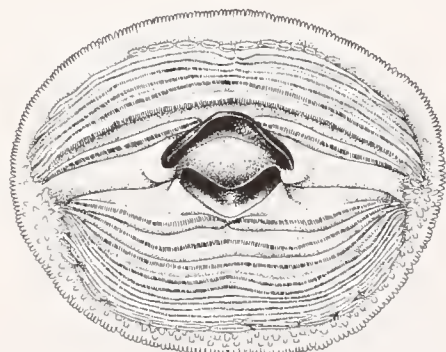


FIG. 219. Mouth of presumed tadpole of *Hyla mixe*, K.U. No. 104183. $\times 8$.

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